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THE MINIMUM TEMPERATURE FOR GROWTH OF THE DATE PALM AND THE ABSENCE OF A RESTING PERIOD [1]

By SILAS C. MASON

Horticulturist, Office of Crop Physiology and Breeding Investigations, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

The culture of the date palm is a relatively new industry in the United States, though scattering trees grown for ornamental purposes or for domestic fruit supply have been known for many years in Southern California and Arizona and in the Gulf Coast regions. The first established date gardens in the United States where systematic observations could be made on the relation of the date palm to climatic environment were planted during the early years of the present century. The date-growing regions of the Old World are generally so remote from the centers of scientific research that definite published observations on the temperatures have been meager. The empirical knowledge of the natives as to the success or failure of their date varieties under different climatic conditions is often very accurate, but as yet little of this knowledge has been coined into a general circulating medium. In our own country the mistake is often made of assuming that where the date palm as a tree is successfully grown its commercial culture for fruit must be equally successful.

Twenty years of observation of the date palm in relation to temperature have established clearly the fact that *Phoenix dactylifera* as a species represented by the cultivated varieties has very definite temperature requirements which must be provided, often within very narrow limitations, if cultural success with a particular variety is to be secured. The zero point, or the temperature below which the growth of date palms ceases with prolonged exposure, seems to be the foundation upon which all study of its other temperature relations should be based. The relative temperature efficiency of two localities in which the date palm is able to grow will be measured most accurately, not by the summation of heat units above zero F. or zero C. but above the zero point of the date palm's activity, which has heretofore been but imperfectly known. For this reason the writer's studies of the zero point of the date palm, both under field and laboratory conditions, are offered here in advance of the studies of the more general relations of this species to climatic conditions.

[1] Received for publication Sept. 26, 1924; issued October, 1925.

THE ZERO POINT OF VEGETATIVE GROWTH

The accurate determination of the zero point, or specific temperature below which all growth of the date palm would cease, is a laboratory problem involving the possibility of the nicest temperature control and the elimination of the effect of sudden temperature variations. With the most favorable conditions for experimenting provided, it would probably be found that the zero point is not constant for the species but varies with the varieties and with the individual plants, so that if a zero point for the species were assumed from results of the study of one variety, it might be but a matter of time until it would be demonstrated that another variety begins its growth at a slightly lower temperature.

For the purpose of this paper, cessation in pushing up of the inner leaves from the bud of a date palm at the normal period of the day will be assumed to indicate a dormant condition of that tree.

De Candolle evidently expected the date tree to enter a resting period somewhat independently of temperature conditions, for he writes regarding it as follows: [1]

> Vegetation probably ceases to be active during the winter, but on a tree which retains its leaves this period is necessarily not well defined. . . . Its vegetation ought to be greatly retarded after fruiting. It is the ordinary physiological law, furthered by the lowering of the temperature. For how long does this resting last? At what average heat will the activity of the tree begin again in the spring? This is what is necessary to know, but positive observations along this line are lacking.

The growth records at Indio, Calif., and at Tempe, Ariz., however, show that growth ceases only (1) under destructive minimum temperatures of about 20° F. or lower, and (2) when zero point maximum temperatures are reached. With accurately marked active leaves under daily observation at the Indio date garden, it was determined that slow growth was made when minimum temperatures dropped below the freezing point, even down to 22° or 21°, provided the day's maximum temperatures were well above 50°. This proved that such low temperatures, if not prolonged, did not in themselves wholly check growth. The short duration usual to such minima prevents penetration to the growth center of the tree. If, now, with minimum temperatures above the freezing point, low maximum temperatures occur, followed by cessation of growth, this result may be logically attributed to the low maxima and a zero point indicated.

ZERO POINT RECORDS AT INDIO, CALIF.

In the autumn of 1916 records of daily leaf growth were begun on four date palms in the United States date garden at Indio, Calif., the growth data in the accompanying tables being the average daily pushing up from the bud center of five active young leaves. These growth records could be coordinated with standard thermometer and thermograph records taken in a standard weather bureau shelter a short distance from the trees. In these records the writer was fortunate in obtaining, in December, 1916, and January, 1917, records of temperatures associated with a sharp decline and finally

[1] CANDOLLE, ALPH. DE. GÉOGRAPHIE BOTANIQUE RAISONNÉE. v. 1, p. 371. Paris. 1855.

the complete cessation of growth in the date palms under observation, which afford the closest approximation to the specific zero point that has yet been secured under field conditions.

After the mild weather and free growth of November and early December, the temperatures from December 7 were decidedly lower (fig. 1, Table I). For 12 days, from December 8 to 19, inclusive, while the mean maximum was still 68.8° F., there were 11 minimum records below 32° and the mean of the minima was 27.8°. There were 4 mornings with a minimum of 25°, and the lowest point reached was 21° on December 10. The retarding influence of successive minima almost continuously below the freezing point was very evident in the early part of this period.

TABLE I.—*Temperature and daily growth records of varieties of date palm, Indio, Calif., December, 1916*

[Critical low temperatures and approximation to zero of growth are indicated by boldface type]

Date	Temperature			Mean daily growth of varieties			
	Maximum	Minimum	Mean	Asherasi	Deglet Noor	Thoory	Zaheedy
	° F.	° F.	° F.	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Dec. 1	73	44	58.5	12.7	11.70	9.20	5.20
2	72	41	56.5	11.9	13.50	9.70	4.60
3	76	55	65.5	7.6	11.70	9.70	4.50
4	75	52	63.5	13.0	14.00	10.00	6.70
5	79	47	63.0	12.5	14.50	11.10	8.00
6	73	48	60.5	12.0	15.30	10.90	8.00
7	61	35	48.0	7.0	11.40	10.40	7.40
8	62	**26**	44.0	10.7	12.30	10.50	5.70
9	65	**25**	45.0	7.0	6.90	4.80	2.70
10	68	**21**	44.5	3.6	2.60	4.10	1.50
11	65	**25**	45.0	2.7	1.90	2.40	.50
12	67	**25**	46.0	5.4	1.60	2.50	1.00
13	74	30	52.0	5.0	**.30**	2.10	**.25**
14	79	35	57.0	3.2	1.20	1.60	.75
15	73	28	50.5	3.4	2.20	1.80	.90
16	73	25	49.0	3.4	2.10	1.10	1.30
17	69	28	48.5	2.4	2.80	2.40	1.06
18	72	31	51.5	5.4	1.60	1.60	1.06
19	67	27	47.0	5.6	3.00	1.70	1.00
20	65	40	52.5	3.2	.65	1.16	.80
21	71	34	52.5	5.9	1.90	1.75	.40
22	68	37	52.5	4.5	2.60	1.80	1.10
23	65	36	50.5	3.6	2.10	1.10	1.20
24	68	40	54.0	2.7	2.50	1.75	.70
25	55	38	46.5	2.7	2.50	1.75	.70
26	**48**	**30**	**39.0**	2.7	2.50	1.75	.70
27	**53**	**32**	**42.5**	.4	.43	**.30**	**.12**
28	**52**	**28**	**40.0**	1.2	1.30	1.60	**.12**
29	58	38	48.0	**.3**	**.21**	**.16**	**.30**
30	67	38	52.5	.0	.65	.07	.00
31	59	29	44.0	(a)	(a)	(a)	(a)
	b 66.8	b 34.4	b 50.6				

a No record obtained. b Mean for the month.

The decline was most marked after the minimum temperature of 21° F. on December 10, and by December 13 the Deglet Noor and Zaheedy trees showed but a fraction of a millimeter in growth, proving that for the conditions in which they were at that period 21° was very nearly a growth-inhibiting minimum.

With the rise of the means from December 13 to 24 a little recovery was made in spite of several frosty nights, so that the depression in growth from December 26 and 27 practically to zero of growth on the

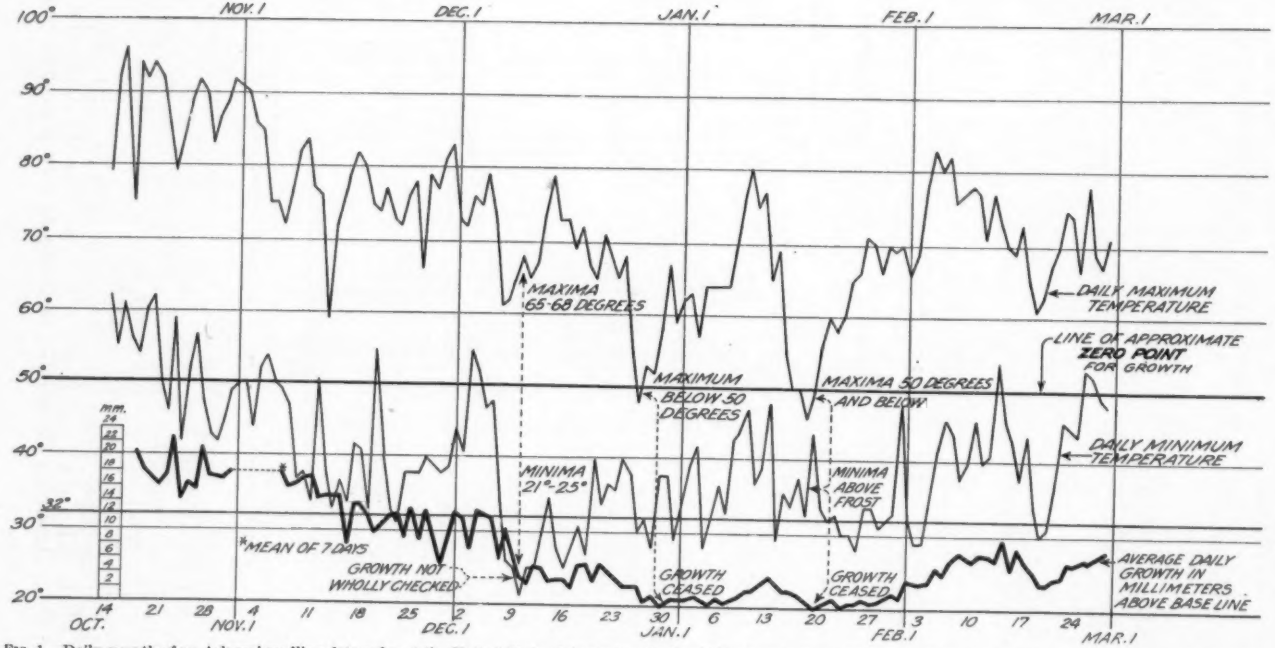


FIG. 1.—Daily growth of an Asherasi seedling date palm at the United States date garden, Indio, Calif., from October 17, 1916, to February 28, 1917, with accompanying maximum and minimum temperatures

30th must be credited to the lower maxima. As the minima of this period were from 28° to 39° F., a little higher than those of the recovery period from December 13 to 18, the way is fully cleared for a zero point determination. The sharp check in growth was recorded on the morning of the 27th following the maximum of 48° at 2 p. m. on the 26th. A little recovery was made on the 28th, but the record of the night following shows a check in growth to a fraction of a millimeter on all trees, and all but the Deglet Noor tree show practically zero point of growth on the 30th. It is evident that the conditions of the observations do not enable one to decide positively whether it required all of the 48° to inhibit growth, or whether 50° or 51°

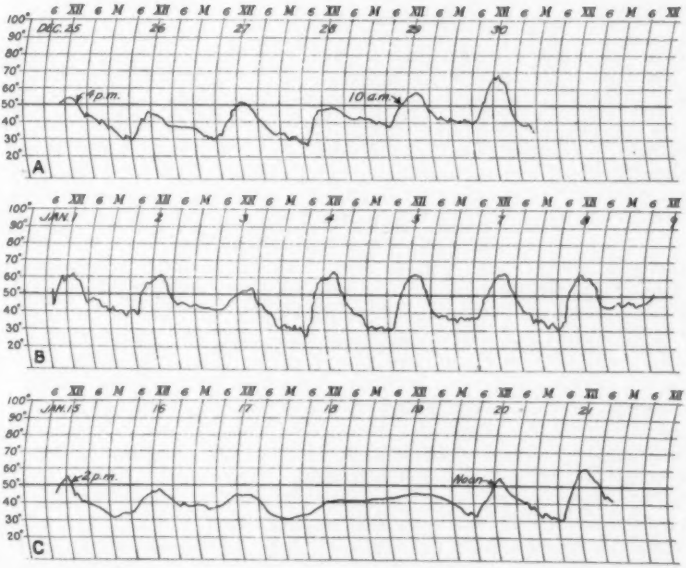


FIG. 2.—Transcripts and thermograph records at the United States date garden, Indio, Calif., covering the critical periods in zero point determination of Tables I and II and Figure 1. A, the hours when the temperature was below 50° F., December 25 to 30, inclusive; B, a similar record for January 1 to 9, and C, for January 15 to 21

would have accomplished this result. This period must be given its weight with the other records.

The period of exposure of the plants to a temperature of 50° F. or below was longer than is apparent from the tables. Reference should here be made to the transcript from the thermograph sheet for December 25 to 30 (fig. 2, A) which, while varying a little from the records of the standard maximum and minimum thermometers, affords on an occasion like this a most illuminating exhibit of the temperatures to which the plants were actually exposed. Assuming the minimum temperature for growth to be 50°, the graph shows for how long a period the temperature was below the 50° line and how little value the very short period of 2 or 3 degrees above 50° in the middle of the day could have had.

INDIO THERMOGRAPH RECORD, DECEMBER 25–29, 1916

The thermographic record at the Indio date garden for the week ending January 1 shows that the temperature fell to 50° F. at about 4 p. m. December 25, and remained below 50° until 10 a. m. on the 29th, except for brief periods on the 27th and 28th, giving a total as follows:

Summation, 50° F. or below:	Hours
December 25	8
December 26	24
December 27	21
December 28	23
December 29	10
Total	86

The January records shown in Table II throw still stronger light on this question. After the entire cessation of growth December 31, all the varieties except the Zaheedy made a slight recovery at once when the maximum temperature rose above 60° F. and there were no frosts. There was a minimum of 28° on January 4 and a record of heavy frost and a minimum of 32° on January 5. With daily maxima of 64° it is difficult to explain a drop to zero in growth of all but the Asherasi on the 7th without the aid of the thermograph record, but an analysis of the thermograph trace for seven days makes the action clear (fig. 2, B). The temperature fell below 50° at 5.30 p. m. December 31, and until 6 a. m. January 7, when the zero of growth was again recorded, there were 159½ hours, of which for 115½ hours the temperature was below 50° and 44 hours (or only 27 per cent of the time) was above 50°. Here was a case where without severe minimum temperatures the long hours below 50° prevailed over the short hours of the day temperatures above 50°. Here the mean temperatures of from 46° to 51° became zero point temperatures, though from January 15 to 21 a mean of 44° was needed to accomplish the same result.

Increasingly warm days through the 14th, with maxima ranging from 69° to 80° F. and minima well above the frost line, except 29° on the morning of the 14th, brought a return of activity so that daily growths of from 1 mm. to 4 or 5 and even exceptional cases of 6 to 9 mm. were recorded.

The 12 days' record from January 14 to 25, inclusive, is so significant as to deserve a close study in the table.

The four days January 16 to 19, inclusive, with minimum temperatures of 33° to 44° but with their maximum of only 46° to 50° F., a second time gives us the clue to the zero point, for after a lag of two days growth entirely ceased on the Zaheedy tree (apparently having the highest zero point of the four) on the 18th. Deglet Noor and Thoory both showed slight growth gains on the 18th, 19th, and 20th, but came to a full stop on the 21st. The zero point in temperature had evidently again been reached, and the four days at 50° and below are as near that point as can be determined under field conditions.

TABLE II.—*Leaf growth record of date palms at Indio, Calif., January, 1917*

[Critical low temperatures and approximation to zero of growth are indicated by boldface type]

Date	Temperature			Average leaf growth per day			
	Maximum	Minimum	Mean	Asherasi	Deglet Noor	Thoory	Zaheedy
	° *F.*	° *F.*	° *F.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Jan. 1	62	34	48.0	1.03	0.85	0.70	0.56
2	63	39	51.0	.93	1.43	1.25	.56
3	57	42	49.5	1.40	.91	1.00	.00
4	64	28	46.0	.93	1.07	.33	.00
5	64	32	48.0	.43	1.43	.66	.31
6	64	37	50.5	1.30	.64	.90	.50
7	64	33	48.5	.50	.00	.00	.00
8	60	43	51.5	1.00	.71	.25	.80
9	76	44	60.0	1.40	1.21	1.33	.30
10	80	47	63.5	2.20	1.43	1.16	.62
11	75	37	56.0	2.40	2.60	1.90	.94
12	77	39	58.0	3.40	3.70	1.90	1.56
13	65	48	56.5	4.30	4.00	2.00	1.30
14	69	29	49.0	3.40	4.00	2.80	1.30
15	55	36	45.5	2.30	4.40	2.76	1.30
16	**50**	**34**	42.0	2.14	1.86	1.83	.87
17	**50**	**38**	44.0	1.60	1.50	1.83	.81
18	**46**	**33**	**39.5**	.50	.64	.66	.00
19	**49**	**44**	46.5	.00	.50	.33	.00
20	56	34	45.0	.00	.43	.50	.00
21	60	32	46.0	.50	.00	.00	.00
22	58	33	45.5	1.20	1.30	1.16	.30
23	60	30	45.0	.14	.80	.75	.25
24	65	30	47.5	.50	.64	.75	.25
25	66	28	47.0	.50	.70	.93	.00
26	71	34	52.5	1.20	.84	.44	.50
27	70	34	52.0	.90	.72	.44	.50
28	66	31	48.5	1.26	1.10	.38	.40
29	70	32	51.0	1.80	1.50	.87	.80
30	69	33	51.0	2.10	2.00	1.20	.66
31	70	48	59.0	1.50	2.00	1.20	1.00
	• 63.6	• 36	• 49.8				

• Mean for month.

The tardiness of the Deglet Noor and Thoory trees in coming to full cessation of growth, with the fact that the Deglet Noor maintained some slight gain throughout the December period, suggests that if 50° F. is the zero point for the Zaheedy seedling, which represents the more tender Persian Gulf varieties, Deglet Noor and Thoory may have a zero point a little lower, possibly 48°; for it is to be expected that within the range of individuals and varieties of *Phoenix dactylifera* there may be a zero point difference of several degrees.

Again the thermograph sheet shows the actual time of exposure of these trees to the low maximum.

INDIO THERMOGRAPH RECORD, JANUARY 15–21, 1917

On January 15, after the temperature had been below 50° F. since 5 p. m. of the 14th, the maximum was 50° to 52° (maximum thermometer 55°) from 10 a. m. until about 1.30 or 2 p. m. From that time the temperature was 50° or below until noon of the 20th, giving a total as follows:

Summation, 50° or below:	Hours
January 15	10
January 16	24
January 17	24
January 18	24
January 19	24
January 20	12
Total	118

ZERO POINT RECORDS AT SAN ANTONIO, TEX.

Further evidence that the date palm zero point can not be above 50° F., and a hint that for some varieties it may possibly lie a little below that point, is found in the records secured on three seedling trees at the United States experiment farm at San Antonio, Tex., in March, 1917.[3] Table III shows temperature records of standard United States Weather Bureau thermometers and corresponding daily growth of one leaf on each of three 8-year-old seedling trees for the first seven days of March.

TABLE III.—*Temperature records and corresponding daily growth at San Antonio, Tex., of one leaf on each of three 8-year-old seedlings for March 1 to 7*

[Critical low temperatures are indicated in boldface type]

Date	Temperature			Growth		
	Maximum	Minimum	Mean	Tree 1	Tree 2	Tree 3
	°F.	°F.	°F.	Mm.	Mm.	Mm.
Mar. 1	74	44	59	20	18	14
2	53	41	47	6	4	5
3	59	41	50	3	4	3
4	**46**	**32**	39	3	1	2
5	**50**	**22**	36	2	1	1
6	61	31	46	2	2	2
7	80	46	63	1	1	1
8	70	38	54	5	3	1
9	73	39	56	5	5	4
10	69	58	63	9	6	4
11	84	64	74	21	11	13
12	81	67	74	22	12	15

After a maximum of 75° F. on February 28 (fig. 3) the thermograph trace crossed the 50° line at 4 a. m. of March 1 and remained at 4° to 6° below it until 10 a. m. of March 2. It passed above the

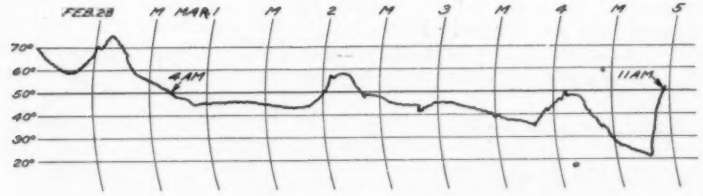


FIG. 3.—Transcript from a thermograph record from February 28 to March 5, 1917, at the United States experiment farm at San Antonio, Tex. The recording instruments were near the date palms from which the growth records in Table III were obtained

50° line at noon March 2, ranging up to 59°, and dropping below it at 8 p. m. It remained below 50° throughout the 3d and 4th, dropping to 22° at 7 a. m. of the 5th, but reaching 50° at 11 a. m.

[3] For the careful keeping of these records the writer is indebted to N. H. Mercier, of the Office of Western Irrigation Agriculture, Bureau of Plant Industry, U. S. Department of Agriculture.

Summation of hours 50° F. or below of the thermograph record in Figure 3

	Hours	
Mar. 1, 4 a. m. to midnight	20	
Mar. 2, 12 midnight to noon	12	
Mar. 2, 8 p. m. to midnight	4	63 hours continuous.
Mar. 3, midnight to midnight	24	
Mar. 4, midnight to midnight	24	
Mar. 5, midnight to 11 a. m	11	
Total	95	

This makes a time lapse of 103 hours, of which 95 hours were below 50° F. and only 8 hours, on March 2, above this temperature. The depressing effect of this period reduced the daily leaf growth from 20, 18, and 14 mm., respectively, on the 1st of March to 2, 1, and 1 on the 5th and (after a characteristic lag) to 1 mm. each on the 7th; but it is to be noted that zero of growth is not completely reached even with this 95-hour exposure to a temperature below 50°. It must be remembered that these were seedling trees of unknown parentage, with the possibility of a lower zero point than those observed at Indio, and the fact of their failure to come to a completely dormant stage still leaves the absolute zero point for the species yet to be established. With the return to higher temperatures recovery was prompt, and the previous growth rate was surpassed on the 11th and 12th.

These widely dissociated and independent records of date-palm growth at Indio and San Antonio, all indicating that the lowest temperature limit for growth lies somewhere at from 48° to 50°, become so cumulative in value that only a laboratory test of the temperature at which growth will cease under prolonged exposure can add to their conclusiveness.

So long as maximum temperatures of 48° to 50° F. are accompanied on the same days by minimum temperatures from 5° to 18° lower, as has been the case on the crucial days at both Indio and San Antonio, it is not safe to affirm positively that the point of cessation of growth in the date leaves has not been in some measure influenced by the lower temperatures.

The fact that under field conditions growth has been made with similar or lower minima but with higher maxima makes the presumption a strong one that the zero point of growth is reached at a definite maximum temperature of the day, which becomes the minimum for cell activity. When laboratory conditions permit of exposing a plant to a very narrow range of temperature, the point at which growth ceases after a considerable exposure may be accepted without further question as the physiological minimum or zero point for growth of that plant.

Reference should here be made to the article by A. E. Vinson,[4] who as early as 1914 made use of the 50° temperature point in studying date-palm growth, but did not, as is shown below, assume this as the actual zero point. As the Tempe Cooperative Date Garden growth measurements were made only weekly, they could not be coordinated with the air temperatures closely enough to secure a real zero point determination.

[4] VINSON, A. E. THE EFFECT OF CLIMATIC CONDITIONS ON THE RATE OF GROWTH OF DATE PALMS. Bot. Gaz. 57: 324-327, illus. 1914.

Vinson, in analysis of weekly growth measurements made for Forbes at the Cooperative Date Garden at Tempe, Ariz., in 1906 and 1907, assumed an "empirical temperature" of 50° F., but on an incorrect hypothesis, for he writes:

> For the present case 50° F. was selected (for the "empirical temperature, below which no marked growth takes place"). This is not to be construed as meaning that no growth would occur at a uniform temperature of 50° F., but under actual climatic conditions the minimum temperature which accompanies a maximum of 50° F. would effectively inhibit growth.

This last conclusion is proved erroneous nearly every winter, for maximum temperatures of 46° to 50° F. with minima above 32° are not rare in the date-palm regions. (See Table II, records of January 16, 17, 18, 19, in comparison with records for December 7 to 12 in Table I.)

During the period covered by Vinson's article the observed palms reached zero growth only during the first week of January, 1906. The official weather records for that time show: January 1, maximum 53°, minimum 29°; January 2, maximum 51°, minimum 19°; January 3, maximum 53°, minimum 18°; January 4, maximum 59°, minimum 20°.

The three days with minima of 19°, 18°, and 20° would alone account for the cessation of growth, leaving the real zero point undetermined.

ZERO POINT DETERMINATIONS UNDER LABORATORY CONDITIONS

Through the courtesy of Frederick V. Coville, botanist of the Bureau of Plant Industry, space was secured in a cool chamber which he had constructed in one of the Department of Agriculture greenhouses in Washington, D. C., where, by means of a small refrigerating machine, the temperature could be controlled within a range of from 3° to 5° F. Three seedling palms of the Thoory variety in 8-inch pots were selected for this work, and after a test of their activity at greenhouse temperatures (about 70° to 80°), were placed one or two at a time in the cool chamber. This cool chamber occupies the position of a greenhouse bench and is about 18 inches deep, 3 feet wide, and 20 feet long. A quantity of saturated sphagnum on its floor insured a rather even condition of high humidity in the air. The greenhouse roof above the bench is shaded during the greater part of the day, so that the light that reached the palms in the cool chamber was considerably reduced in intensity. The temperature of the chamber was recorded by a Richard thermograph, the accuracy of which was checked by a highly sensitive mercury thermometer placed near it.

The governing by the machine thermostat was somewhat erratic and gave a wider temperature range than was desirable. During the main period of 32 days (fig. 4) there was an extreme range from 48° to 56° F. But the time below 50° was only 1.2 per cent of the whole period and the time above 55° was negligible. The mean of the period was, as closely as can be estimated, 53°. The second period, covering five days in which readjustments of the temperature were made, gave a range of from 46° to 54°, the last 48 hours showing a mean of about 49°. During the third and last period of 48 hours, after the thermostat had been again adjusted to a lower temperature, the range recorded was from 44.5° to 49.5°. The peaks of highest

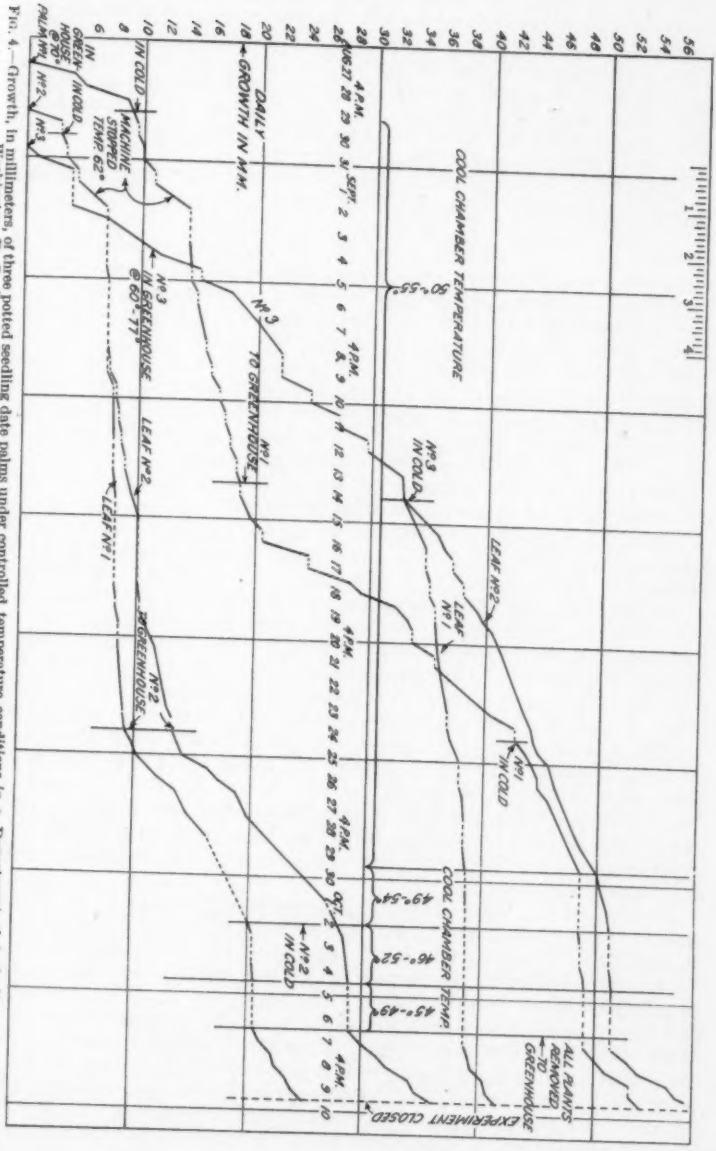

COOL CHAMBER TEMPERATURE
DAILY GROWTH IN M/M.
LEAF Nº2
LEAF Nº1
Nº3 IN COLD
Nº1 IN COLD
Nº2 IN COLD
Nº3 TO GREENHOUSE
Nº1 TO GREENHOUSE
Nº3 IN GREENHOUSE @ 60°-71°
Nº2 GREENHOUSE
MACHINE STOPPED TEMP. 62°
IN GREEN-HOUSE @ 70° PALM Nº3
ALL PLANTS REMOVED TO GREENHOUSE
EXPERIMENT CLOSED
80°-55°
49°-54°
46°-52°
43°-49°
4 P.M.
AUG. 28 29 30 31 SEPT. 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 OCT. 2 3 4 5 6 7 8 9 10

FIG. 4.—Growth, in millimeters, of three potted seedling date palms under controlled temperature conditions in a Department of Agriculture greenhouse in Washington, D. C., from August 27 to October 9, 1918, with index of cool chamber temperatures for the included dates

temperature for this period were quite evenly about two hours apart, the shape of the trace showing only slightly less time in the cooling operation than in the rise to the higher temperature at which the machine started again. The line of 47°, as the mean, divides this trace as equally as it can be done.

Since even in a cold chamber so shallow as this the difference in the temperature between the top and bottom air is considerable, these palms were laid down so as to bring them as nearly as possible on a level with the recording thermograph.

Though palms Nos. 2 and 3 were in turn placed in the cool chamber or used as controls in the greenhouse air, the history of palm No. 1 is so typical that its description will serve for all:

Palm No. 1, with a leaf in active growth, marked for record, was placed in air conditions in the greenhouse at about 70° day temperature and made 9 mm. growth in two days. It was transferred to the cool chamber at 4.40 p. m. on August 29, where, at a mean temperature of 53°, growth dropped at once to 0.5 mm. daily.

Except a short period when the machine stopped and the chamber temperature ran up to 62°, the growth averaged 0.45 mm. daily for 14½ days. Palm No. 3, placed in the cool chamber September 14 under the same temperature range, made 17.4 mm. of growth in 15½ days. This continuous activity under prolonged exposure to these temperatures so near the zero point is an important fact which could not have been disclosed under field conditions.

Palm No. 1 was next transferred to the greenhouse, where day temperatures were 70° to 77°, and made 1 mm. daily gain for two days, then the rate rose to 3 mm. daily. For 10 days under greenhouse conditions the mean daily gain was 2.4 mm. Again placed in the cool chamber September 24, with a temperature averaging 53.5°, this palm made a daily average gain of 1 mm. for the next six days. From noon of September 30 to noon of October 2 the temperature of the cool chamber was lowered to a range of from 49° to 54°, and from noon of the 2d until noon of the 5th it ranged from 46° to 52°. During the first two days no gain in growth was registered, but a gain of 0.6 mm. was made during the following three days at the lower temperature. With the maxima above 50° only six and one-fourth hours, or 8.7 per cent of this time, this close approach to the zero mark is very significant, as a similar reduction in growth was recorded for the two other plants which were in the cold chamber at this period.

Because of the wide range in temperature allowed by the thermostat, it is not certain at this critical period whether this slight growth should be credited to the brief periods when the temperature was above 50° or whether some part of it may have been made at temperatures slightly lower. During the next two days (from noon of October 5 until 9 a. m. October 7), with the temperature ranging from 44.5° to 49.5°, growth on all three plants entirely ceased. Here again the lapse of time during which the temperature was above 49° or below 45° was so small as to be negligible, but the time with the temperature above 48° was six and one-half hours, or 14 per cent of the whole period. This was time enough to have permitted a trace of growth had this been within the growth zone of temperature. By these tests, then, the positive exclusion of growth lies below 49°, with room for doubt whether any growth was made below 50°.

Thus the greenhouse and cool-chamber tests confirm the widely separated field observations in placing the zero point for the date palm at 50° F. or slightly lower. The time of exposure was sufficient for the entire plant (leaves, stem, and roots, with the ball of earth) to have been reduced to the cool-chamber temperature, and we can conclude that the physiological activities which lead to growth were suspended at that point. *The zero point for these palms, then, was the temperature attained by the growing center of the bud at which all growth ceased. We may assume that the same condition holds for large palms in the field.*

At the end of the cool-chamber experiment, after all three plants had been brought to a section of the greenhouse where they had full sunlight and a day temperature of 68° with night minima of 55° to 57°, palm No. 2 began growth during the day, the others the following night, and made gains of from 3 mm. to 8 mm. on the different leaves during the next three days.

These figures clearly show that the plants had sustained no injury by being brought to the zero point of growth. With a slight time allowance necessary to bring the roots in the mass of earth in the pot to the new temperature, they were ready to resume normal activity when exposed to the higher temperature.

With the zero point for constant exposure known, the next step is the application of such knowledge to field conditions, subject to the varying ranges of daily temperature.

Daily mean air temperatures of 50° F. seldom bring the date-palm growth to zero. At Indio a slight growth has been recorded under mean temperatures for weekly periods as low as 45°, but these were where the component maxima were in the 60's and 70's and frost minima were sustained for but brief periods.

At Eureka, Calif., with but few frosty nights and minima rarely below 28° or 30° F., but with monthly means of from 46° to 56° F., giving a normal annual mean of only 51.3°, the growth of the date palm is entirely excluded. At San Francisco, nearly frostless, with monthly means from 49° to 62° F. and the normal annual mean only 54.9°, the date palm makes a slow growth, but seldom, if ever, flowers.

For a comparison of the relative temperature efficiency for the vegetative growth of the date palm of localities not subject to destructive minimum temperatures, if the mean of 50° is taken as the base the monthly summations above that point during the growing season will afford a reliable scale of values.

SUMMARY

The date palm, *Phoenix dactylifera*, as represented by its horticultural varieties, has a wide range of temperature endurance, being able to survive without permanent injury temperatures in different localities from 4° to 125° F.

The geographical range of the date palm as a plant is very much wider than the range of its successful fruit production, and the cultivated varieties are often rather exacting in their temperature requirements.

Date trees, under favorable environment, continue growth throughout the year at a rate closely correlated with the current mean

temperature. Growth may continue at a reduced rate when the minimum air temperatures are several degrees below the freezing point, provided the maximum temperatures of the days are well above a minimum of 50° F.

Observations at the United States date garden at Indio, Calif., show that with minimum temperatures above the freezing point but with the maxima of the days reduced to from 46° to 50° F., growth of four date palms, after a characteristic lag, has been found to have entirely ceased. A specific zero point or minimum of temperature for growth of between 46° and 50° F., but varying slightly with the individuals, has been deduced from these records.

Young date palms in pots placed for 14 days in a controlled temperature bench in a greenhouse at a temperature varying but slightly from 53° F. made daily growth of from 0.5 to 1 mm., and slight gains were recorded at from 49° to 50°. Below 49° all growth ceased. The plants experimented with in the greenhouse cool chamber when placed in greenhouse benches at day temperatures of about 68° F. resumed their normal rate of growth in darkness without appreciable delay. The laboratory tests thus confirm the previous field observations.

The conclusion is reached that the zero point, or minimum temperature permitting, growth of the date palm, lies at from 48° to 50° F. for the actual region of cell division and growth, and that this knowledge is fundamental to the study of the reactions of these trees to other temperature conditions.

PARTIAL THERMOSTASY OF THE GROWTH CENTER OF THE DATE PALM[1]

By SILAS C. MASON

Horticulturist, Office of Crop Physiology and Breeding Investigations, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

The date palm (*Phoenix dactylifera*) is the most important member of the great palm family, excelling even the coconut palm in its economic value to the human race. Its culture is one of the most ancient of which we have records, being recognized in Assyrian tablets of very ancient date, and possibly even earlier in architectural decorations in Egypt. Soon after the children of Israel had escaped from Pharaoh across the Red Sea we are told in Sacred Writ [2] that "they came to Elim, where were twelve springs of water and threescore and ten palm trees: and they encamped there by the waters." The springs are there to this day, and some palms. The place is called in the Arab tongue "Ain Musa"—"The Springs of Moses."

In its climatic requirements the date palm is in strong contrast to the coconut palm, which finds favorable environment along tropical reefs and shore lines having abundant rains and an almost saturated atmosphere, yet without excessive temperatures, and which is tolerant of only the very lightest frosts. The date palm, though fruiting in some coastal regions like northern Egypt, requires a practically rainless season for the perfect development of its fruit, and is at its best in hot interior regions having very high temperatures and low humidity. The practical culture of this palm in the northern hemisphere extends southward to about 15° latitude, but ceases where the region of tropical rains begins. In west Africa the commercial production of dates is confined to the region on the south side of the great Atlas range, although beautiful specimens of nonproductive trees may be seen at Algiers and other Mediterranean cities. A small but very significant commercial culture of the date palm is maintained at Elche, in the southeastern part of the Spanish Peninsula, at a latitude just above 38°, the most northerly point of commercial date culture in the world. Nonfruiting trees may be seen at most points along the northern Mediterranean coast, even extending to Venice at 45° on the Adriatic, but fruit production reaches only a latitude of 35° in Mesopotamia, 34° in Persia, and about 30° to 33° in the Punjab in India.

In the United States, to which the cultivated varieties of dates of Africa and Mesopotamia have been transplanted, fruit has been successfully matured only as far north as 30° to 33° in Arizona and about 34° in California, with possibilities of commercial development as far north as 36° or even 38° in the interior valleys. These data show the approximate range of date culture in the northern

[1] Received for publication September 29, 1924; issued October, 1925.
[2] Exodus xv, 27

hemisphere, and indicate the range of temperature and humidity which may be encountered.

Temperature and humidity ranges in the date-growing region of the Nile Valley, from Alexandria and Rosetta on the Mediterranean coast to Khartoum, comprising a practically continuous north-and-south extension of this culture for over 1,000 miles, were shown in diagrams and discussed by the writer in 1914 (*16*).

Port Said and Alexandria represent in their monthly means of from 56° to 80° F. about the lowest temperatures at which commercial date culture may hope to succeed, here accompanied by high humidity, with monthly means of from 64 per cent to 76 per cent throughout the year. Merowe and Atbara in Sudan have nearly the upper temperature limits at which date culture may be conducted, with monthly means of 68° in January and 93° in June. The relative humidity at Merowe is the lowest recorded for a date-producing region, with means on a 15-year record of only 12 to 16 per cent from March to June and an annual mean of 22 per cent.

But even with the great range of adaptability as seen in Egypt, the full measure of adjustment to temperature of which this tree is capable is not attained. In the Salt River and Gila River Valleys of Arizona date palms have survived minimum temperatures of from 9° to 11° F. with the loss of only the exposed leaves, then, pushing up new leaves promptly with the return of warmer weather, have produced abundant crops of fruit in the year following. Nonfruiting seedling date palms in San Antonio, Tex., have survived minimum temperatures of 4° F. with continuous temperatures below the freezing point for more than 48 hours. At the other extreme, maximum temperatures of 121° at the United States Date Garden at India, Calif., have not seriously impeded the growth rate of the leaves of young date palms nor impaired the development of their fruit.

Such facts regarding a tree of the first economic importance invite the closest study of any peculiarities in its anatomical structure and physiological action which may enable it to endure such vicissitudes. The Arab's idea of the wants of the date palm, "Its feet in running water, its head in the fire of the sky," has so often been repeated, that the growing of the tree under such conditions has been accepted as a matter of course. No one seems to have been aware that the widespread, powerful root system, the sturdy and lofty trunk, capped by the single giant bud with its deeply seated growing point, and majestic crown of a hundred leaves, together comprise a remarkable provision of nature for the protection of the embryonic cell tissues against wide extremes of both heat and cold, and furnish a stabilizer of growing-point temperatures for this tree of the desert.

Like all palms, the date palm is endogenous, its growth internal, with no sensitive cambium zone to be exposed to sunscald under the desert heat. Like all but a small group of palms, it has an unbranched cylindrical trunk, the product of the perennial intercalary growth of a single terminal bud, which in this species is of enormous size.

DeCandolle (*5, p. 37*) had the impression that the date palm has a distinct dormant or resting period after its fruit is matured and during the winter months, and he speculated concerning the tem-

[3] Reference is made by number (italic) to "Literature cited," p. 462.

perature under which growth would be resumed in the spring. Brown (*4, p. 65*) also assumes a dormant period for this tree, and says: "The vegetative growth of the trees commences toward the end of April or the beginning of May * * *."

It has been left to later observers, however, to prove that the date palm in favorable habitats has no resting period, but with water supplied to its roots, continues to push up leaves from the growth center throughout the year. Several complete years of observation show that only minimum day temperatures below 50° F., or destructive night temperatures of 21° or 22° will bring this upward growth to a temporary standstill (*17*).

THE AVAILABLE DATA

Two series of observations on the growth rate of date palm leaves through two full years have been kept in the United States. The first, a condensed report of which was published by Vinson (*24*), was made at the Cooperative Date Garden at Tempe, Ariz., including the years 1906 and 1907, under the supervision of R. H. Forbes, Director of the Arizona Experiment Station. These growth measurements were made weekly. The second was a series of daily growth measurements, kept in part by the writer and completed under his direction, begun in October, 1916, and continued through the full years of 1917 and 1918 at the United States Experiment Date Garden at Indio, Calif. An analysis of these records is not in the province of this paper, but there is a striking agreement in the results obtained, considering the remoteness of the two stations, the difference in the ages of the trees studied, and in the soil and water conditions.

Both records agree as to two important facts in the activity of the date palm: (1) Except for very brief intervals under exceptional conditions, growth is continuous throughout the year; (2) the growth curve, which took no account of volume but was a record of the upward growth of the more active leaves of each tree, follows a course generally parallel to the curve of weekly mean temperatures; the growth is very slow when daily means are below 50° F., and the most rapid growth follows the highest means of 90° to 100°.

In Figures 1 and 2 the mean weekly growth and mean weekly temperatures for 1917 and 1918 are plotted on the basis of zero of growth at a mean of 40° (unity at 42°) and a gain of 1 mm. in mean growth for each gain of 2° in mean temperature.

Plotted on this scale the curve of growth rate falls below the heat curve until about the first or the middle of March; holds increasingly above it from April until midsummer when the peak of the growth rate is reached, and continues above it through a mild autumn to the end of the year.

A decline from 65.5° to 53.5° in the latter part of November, 1917 failed to bring the growth curve down to meet the temperature curve.

As for going into a dormant state, as was assumed by DeCandolle, the average growth rate was still 10 mm. daily and with the unseasonable rise of the temperature means to 64° at the end of December, the mean growth rate for the first week of January, 1918 (fig. 2), advanced to 14 mm. daily. The decline of the January, 1918, temperature means from 61.5° to 49°, however, caused a

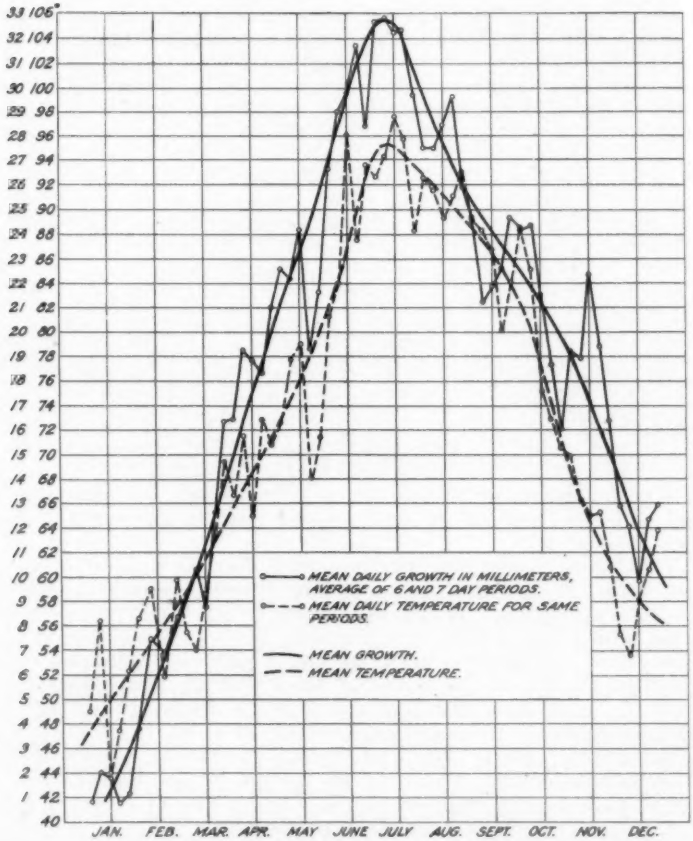


FIG. 1—The relation of the daily leaf growth of four date palms at the United States Date Garden at Indio, Calif., throughout the year 1917 to the daily mean temperature. The temperature is plotted in 6-and 7-day periods and the mean growth in millimeters for corresponding periods on the basis of zero of growth at a mean of 40° and a gain of 1 millimeter in the daily growth rate for each rise of 2° in the daily mean temperature

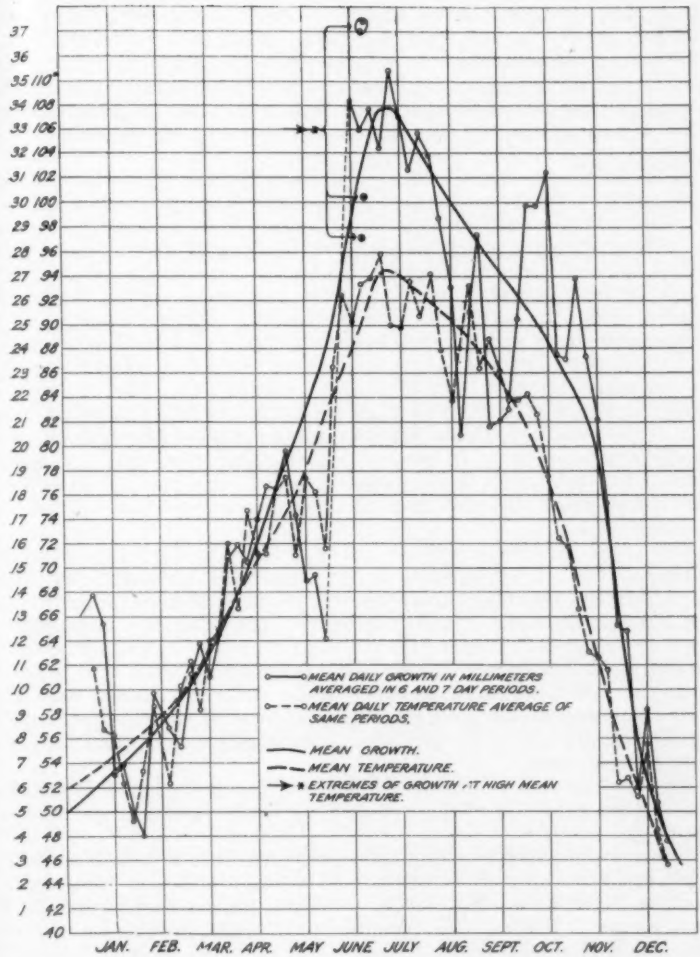


FIG. 2—Corresponding records of growth and temperature for the year 1918. (See fig. 1)

check in the daily growth rate from 14 mm. to 4 mm., but with a quick rising when a temperature mean of 60° was gained, showing the tendency to a perennial growth when the temperature permits.

In other words, though growth in the date palm is sustained throughout the year under Indio and also Tempe temperature conditions, growth is proportionally more rapid at the higher than at the lower temperatures. It will be noticed also that fluctuations of 10° to 20° in the mean temperatures are rather closely followed by corresponding fluctuations in the growth rate, though there are some startling exceptions to this rule in the late autumn growth of both years.

The conditions under which leaf elongation in the date palm is brought to zero are as striking as the fact of its practically all-year growth. While with ordinary plants growth is so nearly confined to "the average frostless season" that "climatic zones" are usually based on such seasonal lengths (*12*) the date palm may show increment in leaf growth when minimum temperatures fall below the freezing point for several days in succession. For example, for three consecutive days at Indio in December, 1916, with minima from 24° to 21° F., growth was not wholly checked when the maxima of those days were above 60°. On the other hand, it was observed twice at Indio in the winter of 1917 that with the minima above the frost line, but with the day's maxima falling below 50°, growth was brought to zero (*17*). In general it may be affirmed that the growth rate in the date palm is more closely coordinated with the temperature throughout the year than that of any other plant species yet studied.

Repeated field observations made by the writer, supported by extended records of growth under controlled temperatures, have demonstrated that the minimum temperature permitting growth of the date palm is close to 49° or 50° F., provided this temperature reaches the growth center (*17*). This zero point of temperature for growth probably varies slightly with different varieties and possibly with the individual tree, growing under different conditions. The zero temperature for growth is rarely reached under the climatic conditions prevailing in date-producing regions, and then only for very short periods.

It is evident that the mode of growth of the date palm is in striking contrast to that of ordinary exogenous fruit-bearing trees, such as the apple, peach, and fig.

Gourley (*8*) found that the total twig growth in a New Hampshire apple orchard under observation in 1916 was practically made during 35 days, from about May 25 to June 30, with a slight gain for 27 days longer. During this time the total daily growth on the observed twigs, computed in sixteenths of an inch, declined from 120 to 10, while the mean daily temperature advanced, measured by a smoothed curve, from about 55° to 75°; yet increase or decrease in daily temperature was followed more or less closely by corresponding changes in growth rate (fig. 3).

The year's twig growth of the apple orchard, chiefly made in a twelfth of the year's time, was in part the expression of the food-building capacity of the last year's leaf crop, and bore only an indirect relation to current temperatures. Increment on a single tree would have been distributed among a network of roots, hundreds of twigs

with thousands of leaves and buds, and a paper-like shell, a veritable cast of the complete tree would have been thrust between last year's bark and wood. Thus the twig growth, in length, was nearly all made in a single month; the addition of the woody shell continued for possibly four months.

DATE PALM STRUCTURE

In contrast with this typical exogenous tree, where the function of cell multiplication and growth is distributed through the cambium zone with its thousands of terminal buds, that of the date palm trunk is concentrated in the single giant terminal bud, or phyllophore,[4] which at the same time is pushing up six or eight great leaves by

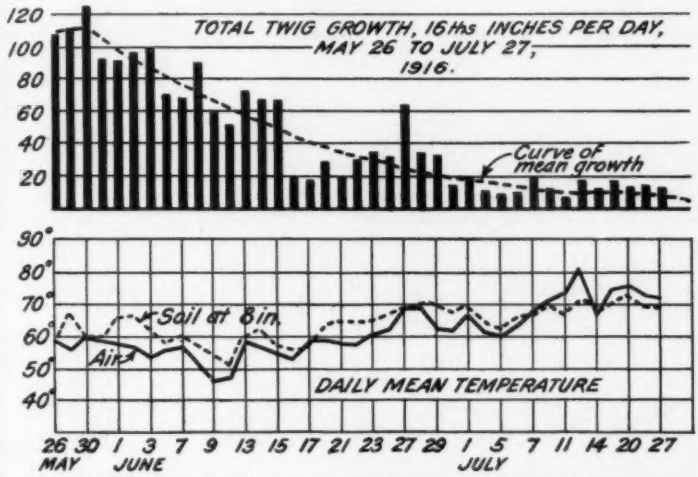


FIG. 3—Total twig growth for the season on selected trees of a New Hampshire apple orchard; below—mean air and soil temperatures for the corresponding period. The twig growth declines from the maximum to zero while the temperature advances

intercalary growth at their bases, laying down flower spathes in their axils for next year's crop, elongating the trunk from 12 to 18 inches a year, and bringing the trunk diameter in the tapering "cone of growth" up to the pattern set by the shaft below. Except at the growing tips of the multitude of ropelike roots, each pushed independently from the sperical base of the trunk, the growth area of this palm is close to the base of the crown of giant pinnate leaves, where the work of photosynthesis is performed and where, under the intense light and dry air of desert conditions, the large volume of

[4] "Phyl'lophor, Phyl'lophore, *Phylloph'orum*, (Φορέω, I carry), the budding summit of a stem on which leaves are developing, especially applied to palms." JACKSON, B. D. A GLOSSARY OF BOTANIC TERMS. Ed. 3, rev. and enl., 427 p. London. 1916.

Apparently this term was first used by Mirbel (*18*) in a communication to the French Academy, Comptes Rendus, 12 Juin, 1843, p. 1216, from which is quoted the following: "Quand on a terminé ce travail, la structure de stipe devient aussi claire que d'abord elle paraissait obscure. En voici la raison: le bourgeon ne peut se développer qu'autant que de nouveaux filets pénètrent dans le phylophore et se dirigent vers les jeunes feuilles."

Martius (*15, p. LXXIV*), who was contemporary with Mirbel and familiar with his work, notices the use of this term as follows: "Illum locum, quem Germani botanici vocarunt gemmae nucleum 'Knospenkern,' novo nomine insignivit Mirbelius 'Phyllophorum'."

water is transpired (pl. 1). This juxtaposition of the region of photosynthesis with the region of cell formation and growth in the date palm has a very important relation to its general activity.

"Centralization of activities" is the keynote of date-palm growth. Its leaves, usually 8 to 12 feet long, are not, as is the case with many palms, loosened from the trunk with maturity, but the bases are strongly attached by tough fiber bundles which penetrate deeply into the cortex. From 10 or 12 to 20 leaves are pushed up from the center of the crown each year. These retain their efficiency four or five years, but gradually turn yellow and dry up, when they are pruned down to within 12 or 15 inches of the place of attachment by the date grower.

The structure of the date-palm leaf is of the greatest importance in securing the insulation of the growth center. The rachis or midrib at the base of the blade, arbitrarily assumed to end at the lowest spines, may be 1 to 2 inches in diameter. From this point the lower portion, considered as the petiole, broadens and thickens more or less rapidly according to the variety and age of the plant. In mature leaves the base may be from 8 to 12 inches broad at the attachment to the trunk, and from 1 to 2 inches thick in the center, thinning out in the lower portion to the marginal thickness of the clasping sheath.

Each leaf petiole has a triple-layered cylindrical sheath from 12 to 20 inches long, at first white and crisp as lettuce leaves, but becoming a tough sheet of diagonally-crossed brown fibers upon expansion and exposure to the light. The line of attachment of the lower margin of the sheath to the trunk marks the beginning of the very short internode of the palm trunk. As the succession of these ribs and sheaths is developed from within, six or eight concentric layers may encircle the phyllophore and their combined strength binds the upper spirals of leaves firmly together [5] against the leverage of the winds on the broad leaf blades. These sheaths, with the persistent heavy fibrous bases, form a most efficient insulating and protecting layer surrounding the delicate meristematic tissue of the growing plant (pls. 2, 3, and 4).

With the crowding up of new leaves in the center the sheath is finally torn from the sides of the base of the petiole, but the successive sheets, attached to the trunk by their lower margins, are tightly wedged behind the encircling bases, 13 nearly vertical ranks of which may be counted around the trunk. In the dry climate of Indio, Calif., and other date growing regions, these bases and sheaths usually persist for many years, covering the entire trunk with a thick mat of dry fiber interspersed with air spaces, and becoming a protective layer.

Plate 1 gives an excellent idea of the external appearance of this protective layer; but Plate 3, a cross section of a date-palm trunk about 2 feet in diameter, shows very beautifully the imbricated arrangement of the spiral succession of leaf bases; while Plate 5, shows how effectively these layers insulate the tender tissues of the phyllophore.

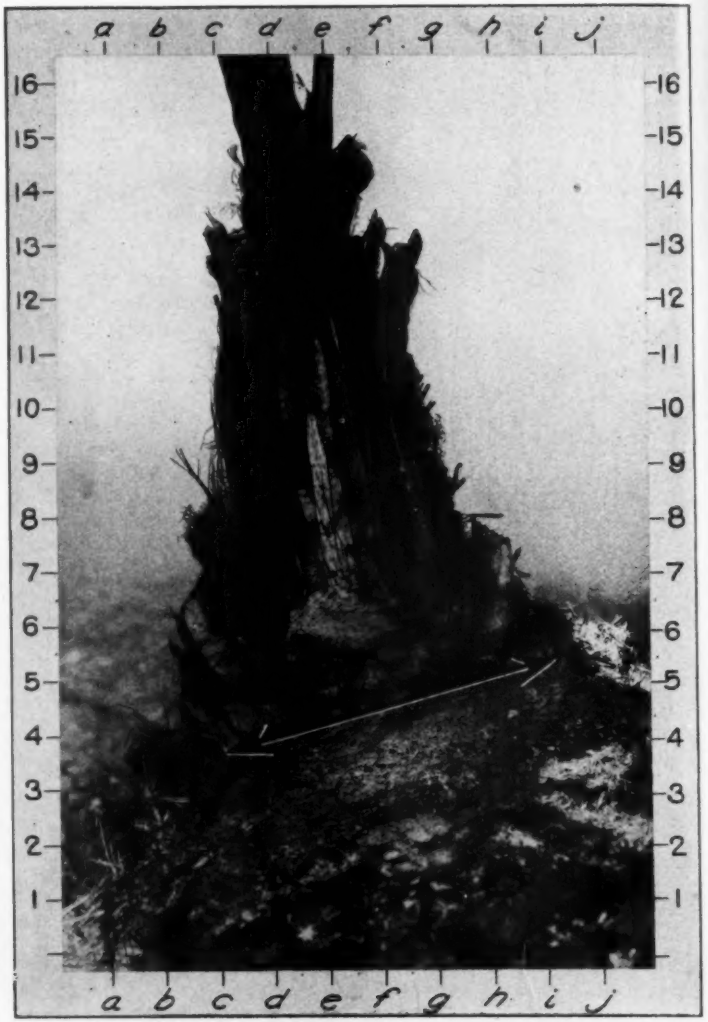
[5] It may occasionally happen that the sheaths bind the apex of the bud so tightly that the new growth of leaves is unable to force its way out.

A general view in the Cooperative Date Garden (University of California and United States Department of Agriculture) at Mecca, Calif. Trees about 15 years old, in full bearing. Tree in right foreground a Deglet Noor. Note the method of emergence of leaves and fruiting stalks from the giant terminal bud and the protective envelope of leaf bases and sheath fiber or "ijef" inclosing the trunk

Top of 10-year-old seedling date palm at Santa Barbara, Calif., which was sectioned to secure plates 3, 4, and 5, showing above *A* a group of newly projected leaves with the pinnae still tightly folded fanwise against the rachis

A cross-section of the trunk of the same date palm shown in Plates 2, 4, and 5, about 23.5 inches in diameter. (See white 10 cm. scale.)

The trunk proper, stained with potassium iodide to show the starch content, is surrounded by the imbricated leaf bases, 7 to 8 inches broad, which form a highly nonconducting protective layer



Above arrow, longitudinal section through the heart of the date palm shown in Plate 2; in front of arrow, horizontal section of half of palm

Print mounted on square ruled paper, ordinates 1–17, abscissa *a–k*

6 to 6.5 *e* to *e* 7, growth center from which group of leaves has sprung by basipetal elongation

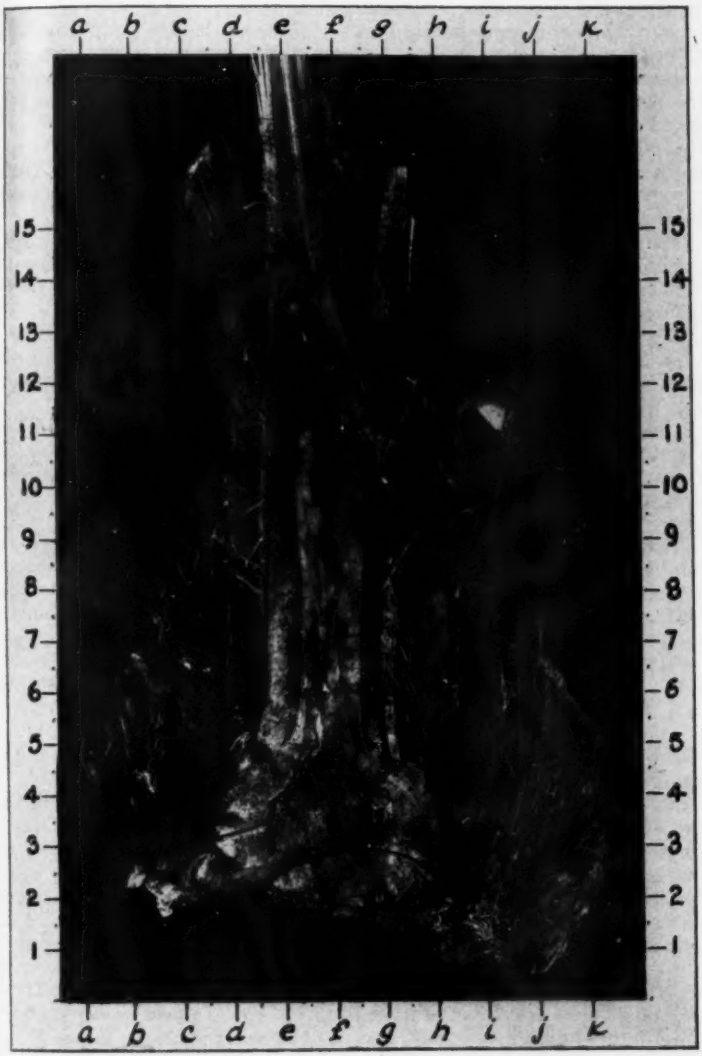
6.5 to 10, with bases *e* to *e* 7, longitudinal section of group of very young leaves. They are pushed upward by growth made wholly within the bud

6.5 to 11.3, breadth *d* 1 to *f*, longitudinal section of bases of group of leaves 4 or 5 feet high, with pinnae still unexpanded, cut tops seen at *c* 5 to *d* 3, also in Plate 2 above *A*. These are making their most rapid growth

6 to 13, breadth *c* 5 to *g*, longitudinal section of bases of older leaves, still making active growth.

5 to 6.5, breadth *d* to *f* 5, very tender, white brittle meristem, giving quick starch reaction. This is the "heart" of the palm that is sometimes eaten. It is at once the growth cap of the trunk and the source of supply of all leaves still making basipetal elongation

2.4 to 6.8, opposite diagonal line showing base of longitudinal section of trunk. In front is the horizontal section of the stump, also showing active starch reaction



The longitudinal half of the palm removed to secure Plate 4, photographed in studio an hour later on a larger scale

The area 2 to 4.7–c 5 to h, is the upper portion of the phyllophore, a mass of meristem, ivory white, and very brittle in spite of the formation of the fibro-vascular bundles, which are here clearly shown, owing to the oxidizing in the air. This is forming the trunk elongation and thickening below while pushing up the new leaves from its apex. The group with their bases at 4.7, in breadth from *d* 5 to *g* 3, are in active elongation, their tops showing above *A* in Plate 2

Their active area of elongation is probably from 5 to 7, but in the region from 8 to 12 the bundles are already well formed, preparing the leaf for exposure to the wind, and for its active service in transpiration and photosynthesis

The growth characters of the date palm may be summarized thus: In the seedling a bulb-like stem pushes up from its growth center by basal increment centripetal spirals of pinnate leaves which make no elongation after they emerge. From the rounded base of this stem is produced an increasing number of cordlike roots which may ultimately reach the thickness of a finger and extend over a radius of 30 to 40 feet or more. They have only small lateral branches and feeding rootlets without root hairs. These roots must convey a large volume of water to the trunk, and at the same time are so provided with fiber bundles that they can support the increasing height of the trunk against the pressure of the wind.

While there is a rapidly increasing production of leaves from the crown until normal development is reached, trunk growth for the first few years is mostly absorbed in increasing the diameter to the size characteristic of the variety, usually from 20 to 30 inches. As the tree advances in height this diameter increment is in progress over a considerable region, so there is always an apical "cone of growth" of varying lengths in different varieties, usually 3 or 4 feet, within which tissue building goes on.

Unlike the old wood or duramen of an exogenous tree in which the sap channels soon become filled up and unable to convey the upward current, the vessels of the date palm trunk remain open and able to convey a strong flow of sap to the crown of transpiring leaves throughout the long life of the tree.

The apical portion of the phyllophore is in a continuous state of subdivision into leaves, which are at the same time pushed to the outside by basipetal elongation and by the upward growth of the central axis. The new leaves are provided with fiber bundles, apparently by the branching of the bundles from below, the main axis continuing in the vertical direction.

We must conceive of growth of the bundles taking place something as in the diagram (fig. 4). The basal portion of the leaves remains in a state of cell division and elongation for many weeks, while the blade as it emerges to the light quickly develops chlorophyll and takes on the characters of permanent or somatic tissues, able to endure the vicissitudes of its surroundings. There is soon established also a differentiation between the leaf tissue and bole or trunk tissue, for while date palm leaves usually retain this attachment to the trunk for a long time, a cross section at any time 2 or 3 feet below the top of the bud shows a well marked difference in structure between the leaf tissue and the trunk tissue. In the physiological action described in this paper a clear distinction must be kept in mind between (1) the protecting envelope comprising the broad bases of the midrib, with the enveloping sheaths, and (2) the trunk proper. These are shown admirably in Plate 3, a cross section of the same palm shown in Plates 4 and 5, at 2 feet above the ground.

There has been much speculation in earlier periods as to the mode of growth and of the development of the fibro-vascular bundles in palms and other plants of the monocotyledonous class, which led to the preparation of papers by Desfontaines, Hugo de Mohl, and other botanists in the latter part of the eighteenth and the early years of the nineteenth century; and in 1839 Mirbel was sent to Algeria by the French Academy of Sciences to study palms in detail. Several of his papers appear in the volumes of Comptes Rendus in 1843–44

and are discussed by Von Martius (*15*). The whole subject was reviewed at length by John Casper Branner (*2*) in 1883, and the results of his own researches in South America given, in comparison with these early theories. Three points in his conclusions have a distinct bearing on the subject of this paper:

(1) This author states (*2, p. 467*):

I would suggest that this development of the fibro-vascular bundles, always in the direction of the apex is due to the light. This apex, at its central point, is very pulpy and translucent while its sides are enveloped in the young and growing fronds which render the parts surrounding the center more or less opaque.

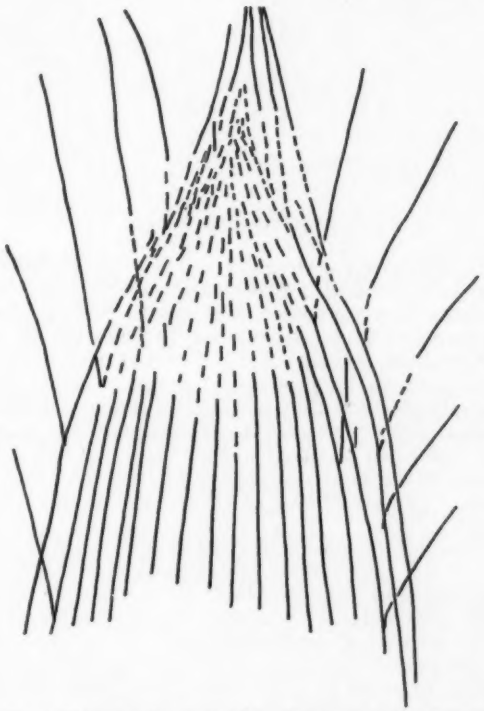


FIG. 4—Diagrammatic representation of the fibro-vascular bundles in the phyllophore of a date palm. Solid lines showing areas in which the bundles have completed their elongation; broken lines, meristematic areas in which the bundles are in process of formation and elongation with branches sent out to the new leaves

Reference should here be made to Plate 5, which shows the reverse half of the palm top cut from that portrayed in Plate 4.

This shows how impossible it would have been for any light to penetrate to the center of the cell division which would have been most active in the area between 4–7 and 1–*g* of the photo scale. The area 2–4+*d*–*h* was, at the time of cutting, ivory white and so brittle that it cracked, as is shown, with the most careful handling. It had been exposed to the air about an hour when photographed and

the oxidizing brought out the tender fibers in strong relief. The early preparation of the leaf to resist exposure to the wind would require this formation of the embryo bundles within the zone of cell division where complete absence of light prevails.

Gradual exposure to the light as the group of leaves is pushed upward would be followed by the completion of the thickening and hardening of these bundles and the full development of the water-carrying tissues, but without gain in length.

(2) Branner also found (*2, p. 470*) that the total number of bundles was about uniform throughout the lower and upper portions of the trunk and that while branches were being continuously given off for the formation and support of new leaves, the number of bundles continuing into the main axis remained substantially uniform.

(3) Branner further states (*2, p. 476*): "A palm trunk may grow laterally as long as the fibro-vascular bundle divisions of the given part are in connection with active fronds." This in practice means that the cone of growth coincides with the altitude zone of active leaves, which is pretty well confirmed by field observations in California and Arizona.

OFFSHOOT BUDS AND FLOWERING BUDS

Morphologically, every date-palm leaf should produce in its axil either a vegetative bud or a fruit bud, though many fail of more than rudimentary development. The earliest buds on seedlings are invariably vegetative buds, giving rise to offshoots so low on the trunk that they often may become self-rooted in the soil. Offshoot buds may continue to be produced for many years, especially in damp coastal climates, but they usually are replaced permanently by flowering buds after a few years. These flower buds may be produced in an almost unbroken succession, but with a heavy production of fruit by the female trees one year, few or no fruit spathes may develop the next year. The staminate and pistillate flowers are borne on separate trees.

The fruit spathes always arise within a few leaves, often only six or eight, of the bud center, and usually develop in centrifugal order, the highest and youngest first, then the next older, spirally downward and outward. All are in closest proximity to the growth center, and the growth of the fruiting stalk is basipetal, as is that of the leaves. Frequently the lower and later flowering heads, though really the oldest in point of origin, seem to be one side of the most active life current and fail to receive the nourishment to bring them to full fruition. This is especially true in the case of male palms, where the late flowers are often abortive.

The interior substance of the young date-palm trunk, when tested has always shown the reaction for starch. To what extent this is a storehouse of reserve food is a question for further study.

The foregoing rather extended account of the structure and habitat of the date tree has seemed necessary to an understanding of the unexpected and remarkable temperature reactions which were observed on inserting thermometers into the heart of the palm trunk—some into the lower trunk and others into the actual growth center.

FACTORS GOVERNING THE INTERIOR TEMPERATURE

The temperature within the massive trunk of a date palm and the phyllophore must be governed by:

(1) The temperature of the surrounding air; (2) the loss or gain of the air temperature in translation through the leaf bases and trunk tissues to the interior; (3) the temperature of the soil at the depth of the feeding roots, assuming that this governs the temperature of the soil moisture as it enters the rootlets and as it traverses the roots to enter the trunk; (4) the loss or gain in the temperature of the ascending sap current in its progress through the trunk to the leaves; (5) an amount, difficult to estimate, of heat generated by the cell activities in the growth center—the heat of respiration.

The factors (1) and (3), both indirectly the products of the air temperature, affect the growth center quite differently; at different hours of the day and during different portions of the growing season. Hence the influence of each should be kept quite distinct in considering the results which follow.

There must also be considered here a factor whose influence we are wholly unable to measure, the cooling effect of the transpiration of the large volume of water from the leaf surfaces. The effect of this in the regions of photosynthesis is undoubtedly considerable. The influence of the return sap current bearing the products of photosynthesis on the general temperature of the phyllophore would be impossible to estimate, but it is probably negligible.

EXPERIMENTAL DATA

In the analysis by the writer of a series of observations on the rate of leaf growth of the date palm in relation to temperature some very significant points were brought to light. It was noted that when the maximum air temperatures were well above 50° F., not only was growth continued after a minimum temperature of 32° was reached, but at temperatures considerably lower; air minima of 25°, 24°, and even of 21° not wholly checking growth on fairly mature trees, though acting more severely on young seedlings. The inference arose that the growing center of a date palm bud must be in some way protected against the actual minimum of cold registered by a thermometer in air near it, unless the cold period is considerably prolonged.

Thermograph records show that minimum temperatures in date-growing regions of California and Arizona last but a few minutes. Shreve (*22*) concludes:

> A consideration of the factors which have to do with the distribution and activities of the giant cactus (*Carnegiea gigantea, Cereus giganteus*) led me to believe that the greatest number of consecutive hours of freezing is the most important climatic datum in determining its northward range, * * *.

While with unicellular plants, as yeast, for example, variations of temperature to which the multiplying cells are exposed may be determined by a thermometer immersed in the culture medium, with most plants which develop tissue systems there is no opportunity to insert a thermometer in the growth centers without such destruction

to cell action as would defeat the end in view, consequently the surrounding air and the soil in which the roots are growing must be relied upon to furnish such determinations.

Fortunately the trunk of the date palm, with its single enormous terminal bud, within which all leaf growth and elongation takes place, affords ample space in which to place a thermometer without serious disturbance to the functions of the plant.

For a study of interior temperatures by this method, a Zaheedy male seedling,[6] one of the trees upon which leaf growth records have been kept at the United States Date Garden at Indio, Calif., was first selected. It had a trunk height of 5.5 feet and a diameter (outside of the leaf bases) of 18 inches at 2½ feet from the ground. At 4 feet from the ground, or 18 inches below the top of the bud, its diameter was 13 inches. Two ¾-inch holes were bored to the center of the trunk, one 18 inches below the apex of the bud, and one on the opposite side of the tree at 30 inches from the ground. A 13-inch chemical thermometer was inserted in each hole after being pushed through perforated corks to close the holes and yet permitting the bulbs to reach the center of the trunk. The bulbs were covered with sleeves of thin rubber tubing to prevent too quick a change in the readings. A third thermometer was installed in a frame close to the trunk of the tree and screened so as to give practically the conditions of a Weather Bureau shelter. A soil thermometer exposed at 2 feet deep in the same grove, 100 yards distant, furnished the soil temperature comparison. Observations were begun at 3 p. m. on February 18, 1918, a heavy snowstorm in the mountains surrounding the Coachella Valley indicating that a sharp frost might be expected on the following morning. Somewhat irregular observations were kept upon these thermometers during the next three months, from early morning till 9 or 10 p. m., in a few instances until a later hour, and one all-night record was made, the readings being taken from a half hour to two hours apart, according to the critical period of the record. Readings of the lower thermometer in the Zaheedy tree were discontinued for a time after March 15, and a second tree, a Maktoom,[6] was used as a check, to ascertain whether the daily curve developed in the temperatures of the Zaheedy tree might be considered characteristic of the species.

These observations, continued until the end of May, became too voluminous for complete presentation within the scope of this article. Five periods of six to eight consecutive days each have been selected as bringing out most effectively the important points disclosed by these studies, and their records tabulated and in part presented in graphs in their relation to current air and soil temperatures.

The readings of the thermometers in the Zaheedy tree from February 18 to 25, inclusive, showing the response to the lowest temperatures encountered, are shown in Table I and the corresponding graphs in Figure 5. Table II shows the records of this tree from March 1 to 6, inclusive, a period when the daily air maxima were 80° F., but with the minima of the last two days suddenly lifted from between 46° and 48° to above 56°.

[6] For convenience referred to as the Zaheedy and Maktoom trees.

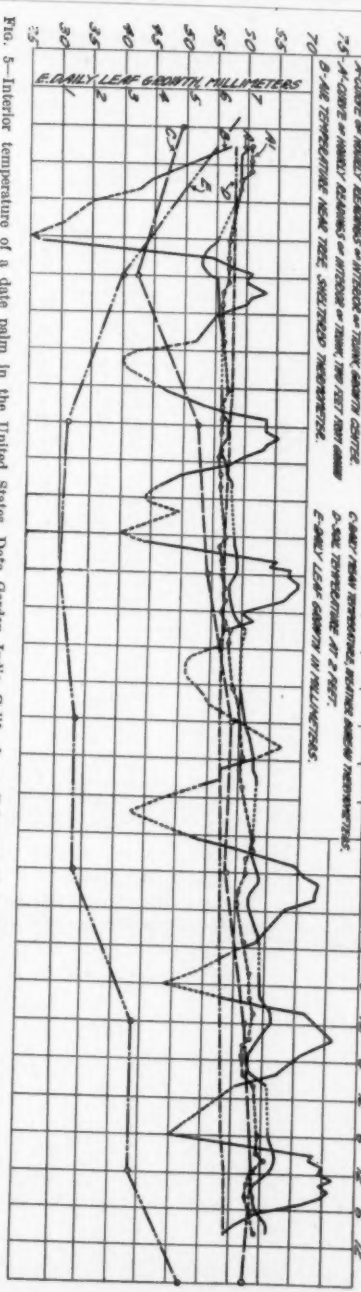

FEB. 18
A-CURVE OF HOURLY READINGS OF INTERIOR OF TRUNK, GROWTH CENTER.
B-CURVE OF HOURLY READINGS OF INTERIOR OF TRUNK, TEN FEET ABOVE GROUND.
C-DAILY MEAN TEMPERATURES, READINGS ABOVE THERMOMETERS.
D-AIR TEMPERATURE NEAR TREE, SHELTERED THERMOMETER.
E-DAILY LEAF GROWTH IN MILLIMETERS.
E. DAILY LEAF GROWTH, MILLIMETERS

FIG. 5—Interior temperature of a date palm in the United States Date Garden, Indio, Calif., from February 18 to 25, 1918, in comparison with air temperature, daily mean temperature, soil temperature at 2 feet, with relative daily leaf growth. (Same tree as in fig. 6)

TABLE I.—*Interior temperatures of the date palm compared with air and soil temperatures of corresponding hours, February 18 to 25*

Time	Air	Soil at 2 feet	Bud zone (by thermometer 1)	Trunk (by thermometer 2)	Time	Air	Soil at 2 feet	Bud zone (by thermometer 1)	Trunk (by thermometer 2)
Feb. 18:	°F.	°F.	°F.	°F.	Feb. 22:	°F.	°F.	°F.	°F.
3.00 p. m.	57.20	.....	60.80	60.80	6.30 a. m.	57.70	.....	60.35	59.00
4.00 p. m.	55.40	.....	59.00	60.80	8.00 a. m.	**54.50**	.....	60.35	59.90
7.00 p. m.	48.20	.....	59.00	60.80	5.30 p. m.	63.50	57.0	62.60	60.80
8.35 p. m.	44.60	58.0	59.00	59.00	7.30 p. m.	57.20	.....	62.60	60.35
10.00 p. m.	42.80	.....	59.00	59.00	9.00 p. m.	57.35	.....	*63.05*	60.80
Feb. 19:					10.00 p. m.	53.60	.....	63.05	60.80
6.25 a. m.	[a]**26.60**	.....	55.40	57.20	Feb. 23:				
9.00 a. m.	54.50	.....	**52.70**	57.20	6.30 a. m.	*53.60*	.....	62.60	*62.60*
10.30 a. m.	57.56	.....	52.70	57.20	8.15 a. m.	60.80	.....	62.15	62.60
11.30 a. m.	60.80	.....	53.60	57.20	9.30 a. m.	65.35	.....	62.60	61.70
12.30 p. m.	59.90	58.0	55.40	57.20	10.30 a. m.	69.35	57.5	63.05	61.70
1.30 p. m.	59.90	.....	55.40	57.20	12.00 a. m.	70.70	.....	63.50	61.60
2.30 p. m.	[b]*65.50*	.....	55.40	**56.30**	1.30 p. m.	73.40	.....	63.95	60.80
3.30 p. m.	60.80	.....	55.40	56.30	3.00 p. m.	72.95	.....	62.60	60.80
4.30 p. m.	59.80	.....	55.40	56.30	4.00 p. m.	72.95	.....	**62.15**	**60.35**
6.00 p. m.	55.40	.....	55.40	56.30	5.30 p. m.	68.00	.....	62.15	60.35
10.30 p. m.	51.80	.....	56.30	56.30	11.00 p. m.	63.50	.....	64.40	61.70
Feb. 20:					Feb. 24:				
6.20 a. m.	**46.40**	.....	56.30	*57.20*	4.00 a. m.	**53.60**	.....	64.40	62.60
9.00 a. m.	53.60	.....	56.30	56.30	8.00 a. m.	58.10	.....	64.40	62.60
10.00 a. m.	58.10	.....	56.30	56.30	10.20 a. m.	71.60	.....	*66.20*	*63.50*
11.00 a. m.	63.50	.....	*57.20*	56.30	12.30 p. m.	72.95	.....	66.20	62.60
12.00 a. m.	63.50	.....	57.20	56.30	2.30 p. m.	*76.10*	58.0	64.40	62.60
1.00 p. m.	63.50	.....	57.20	56.30	3.30 p. m.	74.30	.....	63.50	**61.70**
2.00 p. m.	*65.30*	57.5	57.20	56.30	5.00 p. m.	70.88	.....	62.60	61.70
3.10 p. m.	63.50	.....	56.30	56.30	8.00 p. m.	67.10	.....	**62.60**	61.70
4.00 p. m.	62.60	.....	56.30	56.30	9.00 p. m.	63.95	.....	64.40	62.60
5.00 p. m.	59.90	.....	56.30	**55.94**	10.00 p. m.	60.35	.....	65.75	63.50
6.30 p. m.	54.50	.....	57.20	56.30	Feb. 25:				
8.00 p. m.	50.00	.....	57.20	56.30	5.40 a. m.	52.70	.....	66.30	64.40
9.00 p. m.	48.20	.....	58.10	56.30	6.25 a. m.	**52.25**	.....	66.20	64.40
10.00 p. m.	46.40	.....	58.10	56.30	9.00 a. m.	72.95	.....	*67.10*	64.40
Feb. 21:					10.00 a. m.	72.50	.....	67.10	*65.30*
6.15 a. m.	**43.70**	.....	58.55	*57.20*	11.00 a. m.	74.75	.....	67.10	64.40
7.00 a. m.	43.70	.....	58.55	56.30	12.00 a. m.	74.30	59.0	66.20	63.95
9.45 a. m.	65.30	.....	*59.00*	56.75	1.00 p. m.	*76.55*	.....	65.30	63.50
10.30 a. m.	67.40	.....	59.00	56.75	2.00 p. m.	74.30	.....	63.95	63.05
11.00 a. m.	67.55	.....	59.00	56.75	3.00 p. m.	76.10	.....	**63.50**	**62.60**
12.00 a. m.	67.10	.....	59.00	56.75	4.00 p. m.	74.48	.....	63.95	62.60
1.00 p. m.	*68.90*	.....	**58.10**	56.75	5.00 p. m.	71.60	.....	63.95	62.60
2.00 p. m.	68.90	.....	58.10	57.20	6.30 p. m.	64.40	.....	64.40	63.50
3.00 p. m.	67.55	57.0	58.10	56.75	8.30 p. m.	60.80	.....	66.20	63.50
4.00 p. m.	66.65	.....	58.10	57.20	10.00 p. m.	59.00	.....	66.20	64.40
6.00 p. m.	59.45	.....	58.55	56.75					
7.30 p. m.	61.70	.....	59.00	57.20					
9.00 p. m.	57.20	.....	60.80	**58.10**					
10.00 p. m.	57.20	.....	60.35	58.10					

[a] Figures in bold-face indicate lowest temperatures for the day.
[b] Figures in italic indicate highest temperatures for the day.

TABLE II.—*Interior temperatures of the date palm compared with air and soil temperatures of corresponding hours, March 1 to 6*

Time	Air	Soil at 2 feet	Bud zone (by thermometer 1)	Trunk (by thermometer 2)	Time	Air	Soil at 2 feet	Bud zone (by thermometer 1)	Trunk (by thermometer 2)
Mar. 1:	°F.	°F.	°F.	°F.	Mar 4—Contd.	°F.	°F.	°F.	°F.
6.20 a. m.	[a] **46.40**		62.60	[b] *63.05*	6.30 p. m.	67.55		68.00	65.30
8.00 a. m.	63.95		63.14	63.05	7.30 p. m.	66.65		68.90	65.30
10.00 a. m.	71.60		*64.40*	63.05	9.00 p. m.	64.85		68.90	66.20
12.00 a. m.	73.85		62.60	62.60	10.00 p. m.	63.50		68.90	66.20
1.00 p. m.	*78.35*	60.5	62.60	62.15	Mar. 5:				
3.30 p. m.	76.55		**62.15**	62.15	6.15 a. m.	**56.75**		70.70	67.10
4.30 p. m.	74.30		62.60	62.15	7.00 a. m.	59.45		71.60	67.10
7.00 p. m.	58.10		63.95	**60.80**	7.45 a. m.	68.90		72.50	*68.00*
Mar. 2:					8.20 a. m.	72.05		72.50	68.00
10.00 a. m.	74.30		*65.30*	63.50	9.00 a. m.	72.50		*72.95*	67.55
12.00 a. m.	78.80		63.50	62.60	10.00 a. m.	74.30		72.95	67.28
2.00 p. m.	*79.70*		63.50	62.15	10.30 a. m.	77.45		72.50	67.10
3.30 p. m.	78.80		**63.05**	**61.70**	11.00 a. m.	77.90		71.15	67.28
7.00 p. m.	55.40	61.5	64.40	63.05	12.00 a. m.	79.25		70.34	67.10
9.00 p. m.	57.80		65.75	63.95	1.00 p. m.	77.90	62.5	69.08	66.74
10.00 p. m.	54.50		66.20	63.50	2.15 p. m.	*79.70*		68.54	66.20
Mar. 3:					3.00 p. m.	76.55		68.45	**65.30**
6.15 a. m.	**47.75**		67.10	*65.30*	4.00 p. m.	74.75		**69.36**	65.75
7.15 a. m.	57.95		*67.55*	65.30	5.15 p. m.	71.60		68.36	66.20
11.00 a. m.	78.80		67.55	64.40	6.30 p. m.	67.55		69.80	66.20
1.00 p. m.	79.70	62.0	65.30	63.50	7.30 p. m.	65.30		70.70	67.10
2.00 p. m.	*79.88*		**63.50**	63.14	9.00 p. m.	65.30		71.60	68.00
4.15 p. m.	77.90		63.50	**63.05**	Mar. 6:				
6.30 p. m.	61.25		66.20	63.50	6.10 a. m.	**54.95**		71.78	*69.80*
7.30 p. m.	56.75		66.20	64.40	7.45 a. m.	61.25		71.37	68.90
9.00 p. m.	67.55		67.55	64.40	8.30 a. m.	62.78		72.50	68.90
Mar. 4:					9.40 a. m.	67.55		72.50	68.90
6.10 a. m.	**45.95**		71.60	*67.10*	10.30 a. m.	66.65		*73.58*	68.90
7.45 a. m.	58.55		70.70	67.10	11.00 a. m.	69.80		73.40	68.45
8.45 a. m.	61.70		72.05	67.10	12.00 a. m.	69.98		72.95	68.00
10.00 a. m.	66.65		*72.50*	67.10	1.00 p. m.	69.44		72.05	67.55
11.00 a. m.	71.15		72.50	66.65	2.00 p. m.	*70.70*	62.5	70.70	67.55
12.00 a. m.	75.20		71.15	66.20	3.00 p. m.	69.35		72.05	**67.10**
1.00 p. m.	77.00		69.35	65.75	4.00 p. m.	67.55		69.98	67.10
2.00 p. m.	77.90	62.5	68.00	**65.30**	5.00 p. m.	65.48		**69.80**	67.10
3.00 p. m.	*78.08*		67.28	65.30	6.20 p. m.	63.05		69.80	67.10
4.00 p. m.	77.90		**67.10**	65.30	8.00 p. m.	60.80		71.60	67.10
5.00 p. m.	72.05		67.10	65.30	9.00 p. m.	59.90		71.60	67.10

[a] Figures in bold-face indicate lowest temperatures for the day.
[b] Figures in italic indicate highest temperatures for the day.

Table III shows similar records from March 26 to April 1, inclusive, during which time the minimum air temperatures passed above 60° while the maxima for March 30 and 31 were above 95°. Table IV and Figure 6 show the records of both upper and lower thermometers in the Zaheedy tree for the period from April 21 to 27, inclusive, where the holding down of the temperature of the lower trunk interior is most pronounced.

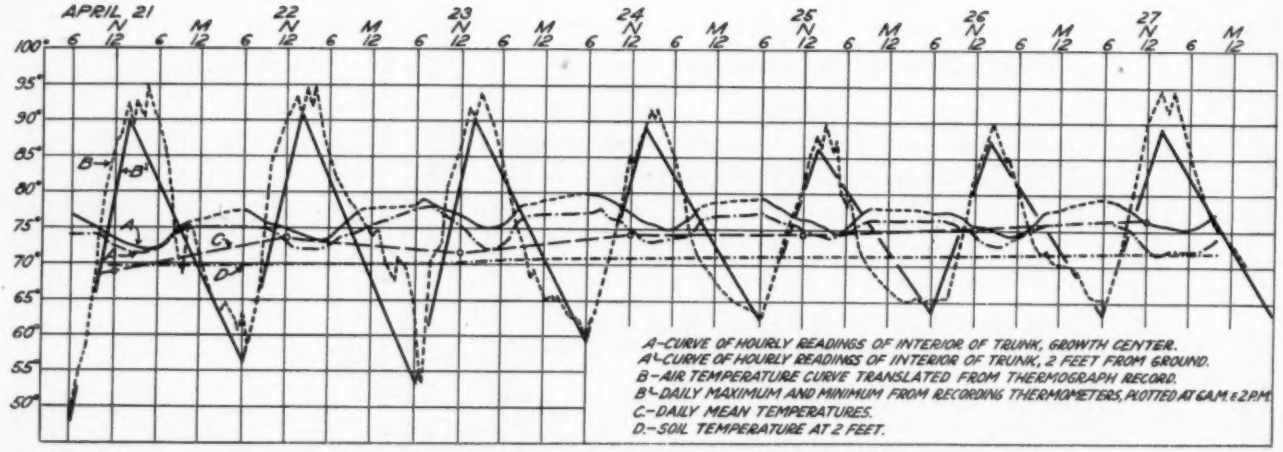


FIG 6—Hourly interior temperatures of a date palm in the United States Date Garden, Indio, Calif., from April 21 to 27, 1918, in comparison with air temperature from thermograph records, daily maximum, minimum, and mean temperature and soil temperature at 2 feet. (Same tree as in fig. 5)

TABLE III.—*Interior temperatures of the date palm compared with air and soil temperatures of corresponding hours, March 26 to April 1*

Time	Air	Soil at 2 feet	Bud zone (by thermometer 1)	Trunk (by thermometer 2)	Time	Air	Soil at 2 feet	Bud zone (by thermometer 1)	Trunk (by thermometer 2)
Mar. 26:	°F.	°F.	°F.	°F.	Mar. 29—Contd.	°F.	°F.	°F.	°F.
5.30 a. m.	[a] **66. 20**	.....	75. 20	*73. 94*	12.10 p. m.	86. 90	.....	71. 60	**68. 90**
6.30 a. m.	66. 20	.....	76. 10	72. 50	1.05 p. m.	89. 60	.....	71. 60	68. 90
9.30 a. m.	72. 50	.....	*76. 28*	73. 22	2.15 p. m.	*90. 50*	66. 0	71. 60	68. 90
10.30 a. m.	75. 20	.....	76. 10	70. 70	3.25 p. m.	88. 70	.....	**70. 34**	69. 80
11.30 a. m.	80. 15	.....	75. 38	69. 98	4.10 p. m.	87. 80	.....	70. 70	69. 80
1.00 p. m.	[b] *83. 78*	.....	75. 38	68. 90	5.00 p. m.	86. 45	.....	70. 70	69. 80
2.40 p. m.	83. 30	.....	73. 22	68. 54	7.00 p. m.	75. 65	.....	71. 60	72. 05
3.45 p. m.	83. 30	65. 0	72. 50	68. 54	8.00 p. m.	70. 25	.....	72. 50	72. 05
4.30 p. m.	82. 40	.....	**72. 32**	**68. 36**	9.00 p. m.	**69. 80**	.....	73. 40	72. 50
6.30 p. m.	71. 60	.....	72. 50	69. 80	Mar. 30:				
7.45 p. m.	70. 88	.....	72. 50	70. 70	5.45 a. m.	**71. 78**	.....	76. 10	*73. 40*
9.15 p. m.	68. 45	.....	72. 50	71. 15	7.30 a. m.	79. 60	.....	*77. 48*	72 95
10.00 p. m.	67. 10	.....	72. 05	70. 70	8.10 a. m.	84. 65	.....	76. 55	72. 50
Mar. 27:					9.00 a. m.	88. 70	.....	75. 38	71. 42
5.50 a. m.	**62. 60**	.....	70. 70	71. 60	10.00 a. m.	89. 60	.....	74. 48	69. 35
6.30 a. m.	63. 95	.....	70. 70	*72. 14*	11.00 a. m.	92. 30	.....	73. 94	.....
7.17 a. m.	66. 65	.....	72. 32	71. 60	12.00 a. m.	*92. 48*	.....	72. 95	**68. 90**
8.00 a. m.	69. 35	.....	*74. 30*	71. 60	1.00 p. m.	92. 48	66. 5	72. 05	68. 90
8.30 a. m.	70. 70	.....	74. 30	70. 70	2.10 p. m.	92. 30	.....	71. 15	68. 90
9.30 a. m.	72. 95	.....	73. 04	70. 25	3.15 p. m.	92. 30	.....	**70. 34**	68. 90
10.45 a. m.	77. 00	.....	72. 68	69. 08	3.50 p. m.	89. 60	.....	70. 52	69. 08
11.50 a. m.	78. 35	.....	72. 50	68. 54	4.30 p. m.	90. 32	.....	70. 34	69. 08
1.00 p. m.	*80. 15*	65. 5	72. 05	68. 90	5.30 p. m.	85. 10	.....	71. 06	70. 25
2.00 p. m.	79. 70	.....	71. 60	**67. 82**	8.15 p. m.	71. 60	.....	72. 95	73. 40
2.30 p. m.	79. 52	.....	70. 70	67. 82	9.00 p. m.	71. 15	.....	73. 40	73. 40
3.00 p. m.	78. 35	.....	69. 98	67. 82	Mar. 31:				
3.50 p. m.	78. 35	.....	69. 44	68. 54	5.00 a. m.	**64. 40**	.....	76. 55	*76. 55*
4.30 p. m.	76. 55	.....	**68. 00**	68. 18	6.30 a. m.	67. 55	.....	*77. 00*	75. 20
6.10 p. m.	70. 70	.....	69. 80	69. 35	8.00 a. m.	79. 25	.....	77. 00	73. 94
7.30 p. m.	68. 45	.....	71. 42	70. 70	8.30 a. m.	82. 85	.....	76. 55	73. 40
8.30 p. m.	65. 75	.....	71. 78	70. 70	10.00 a. m.	92. 30	.....	75. 20	71. 60
9.30 p. m.	63. 95	.....	72. 32	71. 60	11.00 a. m.	93. 20	.....	74. 30	70. 70
Mar. 28:					12.10 p. m.	93. 65	.....	72. 95	69. 80
6.00 a. m.	**52. 70**	.....	73. 22	*72. 32*	1.00 p. m.	94. 55	.....	72. 50	69. 62
7.00 a. m.	68. 45	.....	*75. 02*	71. 42	2.50 p. m.	94. 55	67. 0	70. 70	**69. 35**
8.10 a. m.	72. 50	.....	74. 12	70. 70	4.00 p. m.	*95. 90*	.....	69. 98	69. 35
9.15 a. m.	77. 00	.....	73. 40	69. 80	6.30 p. m.	80. 15	.....	69. 98	69. 80
10.10 a. m.	83. 75	.....	72. 50	69. 80	7.30 p. m.	76. 55	.....	71. 15	72. 50
11.00 a. m.	84. 20	.....	71. 60	69. 35	8.30 p. m.	74. 75	.....	**69. 80**	73. 40
12.05 p. m.	82. 85	.....	71. 60	68. 90	9.30 p. m.	73. 85	.....	73. 85	73. 40
1.10 p. m.	84. 65	65. 5	71. 60	68. 90	Apr. 1:				
2.20 p. m.	*86. 90*	.....	**68. 90**	**68. 45**	6.30 a. m.	**63. 68**	.....	*78. 35*	*76. 55*
3.10 p. m.	86. 00	.....	70. 70	69. 80	7.30 a. m.	65. 30	.....	77. 90	76. 10
4.00 p. m.	85. 10	.....	70. 70	69. 35	8.15 a. m.	68. 36	.....	77. 18	75. 20
5.00 p. m.	81. 05	.....	69. 80	68. 90	9.30 a. m.	71. 60	.....	76. 10	74. 30
7.00 p. m.	69. 80	.....	71. 15	71. 60	10.30 a. m.	75. 65	.....	75. 20	73. 85
8.10 p. m.	64. 40	.....	71. 78	71. 60	11.00 a. m.	77. 45	.....	74. 75	73. 40
9.00 p. m.	64. 94	.....	72. 50	73. 40	12.00 a. m.	*78. 35*	.....	73. 85	73. 94
10.15 p. m.	71. 60	.....	74. 30	*74. 30*	1.15 p. m.	77. 00	.....	72. 95	**70. 70**
Mar. 29:					3.00 p. m.	77. 00	.....	72. 32	70. 70
5.30 a. m.	**56. 30**	.....	73. 40	72. 14	3.30 p. m.	77. 00	.....	72. 14	70. 70
7.20 a. m.	76. 10	.....	*75. 38*	71. 60	4.00 p. m.	75. 65	.....	71. 60	70. 70
8.20 a. m.	78. 44	.....	75. 20	71. 42	5.00 p. m.	72. 95	.....	**71. 42**	71. 24
9.24 a. m.	82. 40	.....	73. 40	69. 80	7.00 p. m.	65. 75	.....	71. 78	71. 78
10.05 a. m.	83. 75	.....	72. 50	69. 80	8.00 p. m.	63. 95	.....	72. 95	71. 60
11.15 a. m.	85. 10	.....	71. 96	69. 35	9.00 p. m.	**63. 50**	.....	73. 40	72. 50

[a] Figures in bold-face type indicate lowest temperature for the day.
[b] Figures in italic indicate highest temperature for the day.

TABLE IV.—*Interior temperatures of the date palm compared with air and soil temperatures of corresponding hours, April 21 to April 27*

Time	Air	Soil at 2 feet	Zaheedy (by thermometer 1)	Zaheedy (by thermometer 2)	Relative humidity	Time	Air	Soil at 2 feet	Zaheedy (by thermometer 1)	Zaheedy (by thermometer 2)	Relative humidity
Apr. 21:	°F.	°F.	°F.	°F.	P. ct.	Apr. 24—Con.	°F.	°F.	°F.	°F.	P. ct.
6.30 a. m.	[a]**49**	.....	[b]*77.00*	*74.00*	27	4.45 p. m.	90	.....	**74.60**	73.00	28
10.00 a. m.	75	70.00	74.50	74.00	.....	5.45 p. m.	86	.....	74.98	73.75	.....
11.00 a. m.	82	.....	74.00	73.00	.....	6.15 p. m.	84	.....	74.90	73.50	.....
12.15 p. m.	87	.....	73.50	72.00	.....	7.35 p. m.	77	.....	75.20	73.50	.....
2.40 p. m.	*92*	69.90	72.50	**71.50**	.....	8.30 p. m.	74	.....	76.00	.....	.....
5.30 p. m.	92	.....	**72.00**	72.00	23	9.30 p. m.	71	70.75	77.60	76.00	.....
6.45 p. m.	88	.....	72.50	72.50	.....	Apr. 25:					
8.20 p. m.	74	.....	74.50	74.75	.....	6.30 a. m.	**63**	71.00	*79.00*	*77.00*	.....
9.00 p. m.	70	.....	75.00	*75.00*	.....	7.40 a. m.	67	.....	78.10	76.30	.....
10.00 p. m.	75	.....	75.00	75.00	.....	8.55 a. m.	72	.....	77.50	75.45	18
Apr. 22:						9.45 a. m.	74	.....	77.00	75.50	.....
6.20 a. m.	**58**	69.90	*77.25*	75.00	.....	10.45 a. m.	78	.....	76.50	75.50	.....
9.00 a. m.	82	.....	75.50	74.75	.....	11.45 a. m.	79	.....	76.25	75.00	.....
10.15 a. m.	86	.....	75.00	74.50	23	12.30 p. m.	82	71.00	76.00	74.50	.....
11.00 a. m.	88	.....	75.00	73.50	.....	1.30 p. m.	87	.....	75.60	74.00	.....
12.00 a. m.	90	70.00	74.50	72.50	.....	2.45 p. m.	*90*	.....	75.00	74.00	.....
1.30 p. m.	93	.....	74.25	72.25	.....	3.45 p. m.	87	.....	74.50	**73.50**	.....
3.00 p. m.	*95*	.....	73.50	**72.00**	.....	4.30 p. m.	85	.....	**74.00**	74.00	37
4.00 p. m.	95	.....	**73.00**	72.00	.....	6.30 p. m.	78	71.00	75.25	74.50	.....
5.00 p. m.	90	70.00	73.00	72.00	18	7.30 p. m.	74	.....	76.00	75.00	.....
7.15 p. m.	84	.....	74.50	73.75	.....	8.30 p. m.	71	.....	77.00	75.80	.....
8.10 p. m.	79	.....	75.50	74.00	.....	9.30 p. m.	70	.....	*77.50*	*76.00*	.....
9.15 p. m.	78	.....	76.50	74.00	.....	Apr. 26:					
10.00 p. m.	77	.....	77.00	74.50	.....	6.30 a. m.	**64**	71.00	77.00	76.00	.....
Apr. 23:						8.00 a. m.	66	.....	77.00	76.00	.....
6.15 a. m.	**53**	70.00	78.00	77.50	.....	9.00 a. m.	70	.....	77.00	75.60	56
7.05 a. m.	57	.....	*79.00*	77.50	57	10.00 a. m.	73	.....	76.50	75.25	.....
8.15 a. m.	72	.....	77.80	*77.98*	.....	11.30 a. m.	81	.....	75.50	74.75	.....
9.30 a. m.	74	.....	77.50	77.10	.....	1.30 p. m.	85	.....	75.00	72.95	.....
10.45 a. m.	83	.....	77.00	76.30	.....	3.00 p. m.	*90*	.....	74.50	**72.50**	.....
11.25 a. m.	85	.....	76.90	76.00	.....	4.10 p. m.	87	.....	74.00	72.95	.....
12.30 p. m.	87	70.00	76.50	75.20	.....	5.00 p. m.	85	.....	**73.75**	73.40	32
1.45 p. m.	92	.....	75.50	73.40	.....	7.00 p. m.	75	71.25	74.50	74.30	.....
2.30 p. m.	*94*	.....	**75.00**	72.20	.....	8.30 p. m.	72	.....	76.00	.....	.....
3.40 p. m.	92	.....	75.00	**72.10**	.....	9.30 p. m.	72	.....	77.00	75.20	.....
4.20 p. m.	90	.....	75.00	72.10	23	10.30 p. m.	71	.....	77.10	75.20	.....
5.30 p. m.	87	.....	75.00	72.30	.....	Apr. 27:					
6.30 p. m.	82	70.50	75.75	73.00	.....	6.30 a. m.	**65**	71.25	*79.00*	*76.10*	.....
7.30 p. m.	77	.....	76.50	75.10	.....	8.10 a. m.	70	.....	78.40	75.38	57
8.30 p. m.	73	.....	77.30	76.00	.....	9.40 a. m.	78	71.40	77.80	74.75	.....
9.30 p. m.	71	.....	78.00	76.50	.....	10.30 a. m.	82	.....	76.75	74.30	.....
Apr. 24:						11.30 a. m.	84	.....	75.90	72.50	.....
6.30 a. m.	**61**	70.50	*79.50*	77.00	.....	12.35 p. m.	86	71.50	75.95	71.60	.....
7.30 a. m.	65	.....	79.00	*77.50*	59	1.45 p. m.	90	.....	75.80	**71.42**	.....
8.10 a. m.	68	.....	78.90	76.90	.....	2.35 p. m.	92	.....	75.80	71.60	.....
9.30 a. m.	73	.....	78.40	76.30	.....	3.40 p. m.	*93*	71.50	75.00	71.60	.....
10.25 a. m.	77	.....	78.10	75.90	.....	4.30 p. m.	92	.....	**74.95**	71.68	.....
11.30 a. m.	80	.....	77.20	74.40	.....	5.30 p. m.	90	.....	74.95	71.60	20
12.45 p. m.	85	.....	76.10	73.80	.....	6.30 p. m.	86	.....	74.95	71.60	.....
1.30 p. m.	88	.....	76.00	73.20	.....	8.30 p. m.	78	71.00	76.00	72.50	.....
2.30 p. m.	*92*	.....	75.50	**73.00**	.....	9.30 p. m.	74	.....	76.75	73.40	.....
3.20 p. m.	91	.....	75.00	73.00	.....						

[a] Figures in bold-face type indicate lowest temperature for the day.
[b] Figures in italic indicate highest temperature for the day.

Table V shows the records of the Maktoom tree at the growth center and of the Zaheedy tree at 2 feet from the ground, from April 28 to May 4, a period when the interior temperature curves both fell mainly below the curve of the mean daily air temperature. Table VI shows temperatures observed in May, 1923, in the trunk of a large seedling male palm at 4 feet from the ground, compared with soil temperatures at 2 feet and 3 feet deep. Here, with an older and more deeply rooted tree, a striking proof of the influence of the ascending sap current is introduced, in that the tree trunk temperature passed below that of the soil at 2 feet for several days, and closely approached the soil temperature given by the thermometer set at a depth of 3 feet.

TABLE V.—*Interior temperatures of the date palm compared with air and soil temperatures of corresponding hours, April 28 to May 4*

Time	Air	Soil	Maktoom (by thermometer 1)	Zaheedy (by thermometer 2)	Mean air
Apr. 28:	°F.	°F.	°F.	°F.	°F.
6.30 a. m..	**64**	70.50	*75.20*	*76.10*	------
7.15 a. m..	67	------	75.20	76.10	------
9.30 a. m..	77	------	75.20	75.20	------
10.40 a. m..	86	71.00	74.75	74.48	------
11.45 a. m..	89	------	74.30	74.30	------
1.30 p. m..	91	------	73.40	**73.22**	76.7
2.45 p. m..	*94*	------	73.85	73.40	------
3.45 p. m..	94	71.00	**72.50**	73.58	------
4.45 p. m..	91	------	73.85	73.40	------
6.30 p. m..	85	------	74.30	74.30	------
7.00 p. m..	82	------	74.50	74.75	------
8.30 p. m..	78	------	75.20	75.20	------
9.30 p. m..	76	------	75.20	75.20	------
Apr. 29:					
6.00 a. m..	69	------	*77.00*	*77.00*	------
6.40 a. m..	**64**	70.75	77.00	76.82	------
8.50 a. m..	80	------	76.10	75.74	------
10.10 a. m..	86	------	75.65	75.20	------
11.50 a. m..	88	------	74.30	75.20	------
2.25 p. m..	95	------	73.85	**71.60**	78.5
3.05 p. m..	*96*	------	**73.40**	71.60	------
4.03 p. m..	95	71.00	73.85	71.78	------
5.00 p. m..	94	------	73.85	72.95	------
6.20 p. m..	90	------	74.30	73.40	------
7.07 p. m..	85	------	74.75	75.20	------
8.30 p. m..	81	------	75.65	------	------
9.30 p. m..	74	------	76.10	76.10	------
Apr. 30:					
6.12 a. m..	**60**	70.00	77.00	*77.90*	------
7.25 a. m..	70	------	*77.18*	77.45	------
9.50 a. m..	83	------	77.18	76.55	------
10.20 a. m..	85	------	76.55	75.60	------
11.40 a. m..	92	------	76.10	75.38	------
1.15 p. m..	*96*	------	75.20	74.75	------
2.15 p. m..	96	------	**74.30**	**72.50**	------
4.25 p. m..	91	------	75.20	73.40	79.0
6.52 p. m..	85	------	76.10	75.20	------
8.00 p. m..	80	70.50	77.00	76.10	------
9.30 p. m..	76	------	78.35	77.00	------
May 1:					
6.30 a. m..	**70**	70.00	*80.60*	*78.80*	------
7.30 a. m..	73	------	78.35	77.54	------
8.30 a. m..	79	------	77.72	77.00	------
9.30 a. m..	85	------	77.45	76.28	------
11.13 a. m..	88	------	77.00	------	------
1.10 p. m..	93	70.50	75.65	74.75	------
3.30 p. m..	*97*	------	**73.40**	**72.50**	------
5.10 p. m..	96	------	75.20	72.95	------
6.30 p. m..	93	------	76.64	73.40	82.5

Time	Air	Soil	Maktoom (by thermometer 1)	Zaheedy (by thermometer 2)	Mean air
May 1—Con.	°F.	°F.	°F.	°F.	°F.
7.45 p. m..	85	70.50	77.36	73.76	------
8.30 p. m..	77	------	78.98	76.10	------
9.30 p. m..	70	------	79.70	76.64	------
May 2:					
6.00 a. m..	**55**	70.00	*80.60*	*77.45*	------
7.30 a. m..	62	------	79.70	77.00	------
8.45 a. m..	74	------	78.80	77.00	------
10.00 a. m..	78	------	77.90	76.82	------
11.00 a. m..	83	------	77.90	76.64	------
12.30 p. m..	90	------	77.00	75.74	------
2.30 p. m..	97	------	77.00	74.75	78.0
3.30 p. m..	99	------	**76.10**	74.30	------
4.30 p. m..	*101*	70.50	76.10	74.30	------
5.30 p. m..	95	------	76.10	**73.40**	------
6.30 p. m..	90	------	76.10	73.58	------
7.30 p. m..	82	------	76.55	73.58	------
8.30 p. m..	73	70.50	77.00	75.56	------
May 3:					
6.00 a. m..	**60**	71.00	*79.25*	*79.70*	------
7.10 a. m..	61	------	79.16	79.25	------
8.30 a. m..	73	------	78.80	78.35	------
9.35 a. m..	80	------	78.35	77.90	------
10.30 a. m..	85	------	77.90	75.65	------
11.30 a. m..	90	------	77.36	75.38	80.0
12.30 p. m..	92	------	77.00	75.20	------
1.40 p. m..	95	------	75.65	75.20	------
2.45 p. m..	*99*	------	75.56	74.30	------
3.45 p. m..	98	------	75.30	**73.76**	------
4.30 p. m..	97	------	**75.20**	73.76	------
5.30 p. m..	95	------	75.20	73.76	------
6.30 p. m..	90	71.00	75.20	74.30	------
7.30 p. m..	85	------	76.10	------	------
May 4:					
6.15 a. m..	**60**	70.60	*80.15*	*79.70*	------
7.30 a. m..	65	------	80.15	78.80	------
8.30 a. m..	75	------	79.70	78.35	------
9.30 a. m..	79	------	78.80	78.08	------
10.30 a. m..	83	------	77.90	78.08	------
11.30 a. m..	85	------	77.00	77.90	------
12.35 p. m..	87	71.50	76.64	76.64	------
1.30 p. m..	90	------	76.55	75.56	------
2.25 p. m..	92	------	76.55	74.93	77.0
3.30 p. m..	*93*	------	**76.10**	**74.75**	------
4.30 p. m..	92	------	76.10	74.75	------
5.30 p. m..	91	------	76.10	74.75	------
6.30 p. m..	87	------	76.55	75.02	------
7.30 p. m..	80	------	77.36	76.10	------
8.30 p. m..	78	71.50	78.44	76.82	------

* Figures in bold-face type indicate lowest temperature for the day
* Figures in italic indicate highest temperature for the day

TABLE VI.—*Interior temperatures of a large seedling male palm compared with air and soil temperatures, May 5 to May 11, 1923*

Time	Air (by thermograph)	Soil at 2 feet	Soil at 3 feet	Interior of trunk (at 4 feet height)	Time	Air (by thermograph)	Soil at 2 feet	Soil at 3 feet	Interior of trunk (at 4 feet height)
May 5:	°F.	°F.	°F.	°F.	May 9—Contd.	°F.	°F.	°F.	°F.
8.30 a. m.	**89**	**72.75**	.....	*73.00*	10.45 a. m.	.....	73.75	*71.55*	73.75
10.00 a. m.	90	*73.00*	.....	72.00	12.00 a. m.	*108*	73.75	71.55	73.50
12.00 a. m.	.....	73.00	.....	71.75	1.30 p. m.	.....	73.75	71.55	**73.25**
2.00 p. m.	[a] *102*	73.00	.....	71.75	3.00 p. m.	.....	73.75	71.55	73.50
4.00 p. m.	.....	73.00	.....	[b] *71.50*	4.00 p. m.	.....	73.75	71.55	73.25
May 7:					5.00 p. m.	105	73.75	71.55	73.50
8.15 a. m.	85	**74.00**	.....	*74.50*	May 10:				
11.00 a. m.	.....	74.00	.....	73.00	8.30 a. m.	87	**74.00**	*72.00*	*75.75*
1.30 p. m.	.....	*74.50*	*72.00*	[b] *72.50*	10.00 a. m.	.....	74.00	71.55	74.00
3.00 p. m.	*110*	74.00	71.10	72.50	11.00 a. m.	.....	*74.25*	71.55	73.75
4.45 p. m.	.....	74.25	71.10	72.50	12.00 a. m.	100	74.25	71.55	73.75
May 8:					1.30 p. m.	.....	74.25	71.55	**73.50**
8.00 a. m.	**90**	*75.00*	*71.10*	*75.00*	3.30 p. m.	*103*	74.25	71.55	73.50
10.00 a. m.	.....	**74.75**	71.10	73.00	5.00 p. m.	.....	74.00	71.55	73.50
11.00 a. m.	.....	75.00	71.10	72.75	May 11:				
1.30 p. m.	*109*	75.00	71.10	72.75	9.00 a. m.	**80**	**74.50**	72.00	*75.50*
2.30 p. m.	.....	75.00	71.10	**72.50**	10.30 a. m.	.....	74.50	72.00	74.25
4.00 p. m.	.....	75.00	**70.65**	72.75	11.30 a. m.	95	74.50	72.00	74.00
May 9:					1.45 p. m.	*102*	74.50	72.00	73.75
8.15 a. m.	**86**	*74.50*	**72.00**	*75.50*	3.15 p. m.	.....	*74.73*	72.00	**73.50**
9.45 a. m.	.....	**74.00**	72.00	74.00	4.30 p. m.	95	74.50	72.00	74.00

[a] Figures in bold-face type indicate lowest temperature for the day.
[b] Figures in italic indicate highest temperature for the day.

THE INVERTED TEMPERATURE CURVE

Tables I to VI and the graphs shown in Figures 5 and 6 indicate a fairly uniform and very significant 24-hour curve of the interior tree temperature. In February and early March a daily maximum was reached at about 9 to 10 or 11 a. m., but as the air temperature means advanced during the latter part of March, this interior maximum occurred about 6.30 a. m., and was maintained but a short time, followed by more or less gradual drop of from 2° or 3° to 5°, or at most 7°, reaching a minimum at from 3 to 5 p. m. From this a rise followed, unless the air temperature had dropped during the day, persisting as late in the night as the readings were taken, which was usually not later than 10:30 p. m., although one record was kept to 12.30 a. m., and one all night. A continuation of this rise was generally traced at 4.30 to 6.30 a. m., making the night temperature curve a part of the approach to the morning maximum.

Whatever the factors may be, tending toward an equalization of the temperature of the growing tissues, the result is an inversion of the temperatures, holding the tissues at their highest point during the coolest morning hours, and at their lowest temperature during the maximum of the day's heat.

NARROW RANGE OF INTERIOR TEMPERATURES

Another matter of interest to be noted in Tables I to VI and in the graphs Figures 5 and 6, is the very narrow daily range exhibited by the interior temperatures as compared with the temperature of the air. During February and the early part of March the 24-hour range shown by the upper thermometer inserted into the growing region of the date trunk was only from 1.8° to 5.4°, and that of the

lower thermometer only from 0.36° to 2.7°, while for the corresponding period the air temperatures range from 21° to 38°. During the last days of March, with maximum air temperatures reaching 94° and 95°, and minima at 60° and 61°, a daily range of 33° to 35°, the 24-hour range of temperatures within the two trees was at most 7.2°.

Next we may note that the tree temperatures were slowly ascending, day by day, at a rate which on the whole corresponded with the rise in the daily mean temperature of the air, tending at first to keep above it, but as the mean air temperature increased, falling below it, but throughout keeping a relatively uniform distance above the soil temperature.

Here it is necessary to consider more in detail the action of the factors (1) and (3), previously outlined, in their control of the temperature of the growth center.

THE AIR TEMPERATURE

Thermographic records show that at the Indio garden, the air minimum is usually reached shortly before sunrise and is maintained but a short time. The upward curve of the trace is a rapid one, often showing a gain of 20° by 9 or 10 a. m., with a maximum for the day 25° to 40° above the minimum; reached at 2 or 3, sometimes as late as 4 p. m. The afternoon decline is much slower than the morning rise, until after sunset, when the radiation through the dry desert air goes on steadily till morning.

The regulatory influence of the daily air temperature naturally falls into two periods—(1) in which the air temperature is below the soil temperature; and (2) that in which the air temperature is above the soil temperature. With the preponderance of the first, the growth center temperature, after the lag in penetrating the protection envelope, is pulled down toward the soil temperature and, if severe enough, is brought below it; the sap, deriving its temperature from the soil, being unable to wholly overcome the penetration of cold from without.

This condition is shown in Table I and Figure 5, where from 3 p. m. on February 18 to 7 a. m. on the 21st, the air temperature was below the soil temperature for 46 hours and above it only 18 hours. This is expressed by the mean temperature line *C* Figure 5, which remained below the soil temperature line until the 22d.

The penetration, through the protecting envelope, was slow, however, and the growth center minimum of 52.7° was only reached at from 9 to 10.30 a. m. The sap, at about the soil temperature, must be credited with overcoming this frost incursion and keeping the growth center temperature a little above the zero point of 50°.

The thermometers show both trunk and bud temperatures below the soil temperature, with a slow recovering on the afternoon of the 21st. The soil temperature, itself, under the influence of the prolonged low air temperature was lowered from 58° to 57.5° and finally to 57°, only getting back to 58° on the 24th after the air temperature curve became higher than the soil curve for a predominant portion of the day.

In successful date-producing regions the periods when the air is colder than the soil are very short and the main problem is with the

air warmer than the soil for a greater part of the day, or ultimately for the entire 24 hours, as is shown in Table VI. An inspection of Tables I to V shows that on a clear day the air is maintained at within about 5° or 6° of the day's maximum for a period of from 5 to 6 hours, and within 10° of the maximum for an average of 7 hours. Upon exposed surfaces the penetration of heat, when the maximum air temperature is 100° or upward, is terrific and the radiation of the accumulated heat from a brick or adobe wall can be felt long after sundown. Vegetation with unprotected surfaces often shows, within the tissues, temperatures several degrees above the surrounding air. Smith (*23*) observed interior temperatures in the giant bamboo, *Dendrocalamus giganteus*, 6° above the surrounding air, which he attributed to "the intensity of the solar radiation incident upon the growing organ." Even greater increment in temperature has been observed in the tissue of the giant cactus upon the deserts of the Southwest. The different conditions found in the interior of the date palm are in most striking contrast.

To sum up the evidence, then, the air temperatures, low or high, are retarded and largely intercepted by the protective layer of leaf bases and sheath fiber, before they reach the merisematic tissues of the growth center or phyllophore. This is a stabilizing effect, tending to prevent the penetration of temperatures below the optimum for cell growth in cold weather, and conversely, retarding the penetration of temperatures above the optimum during periods of extreme heat.

THE SOIL TEMPERATURE

The second factor, derived from the first, is the temperature of the soil at 2 to 3 feet deep, where the greater part of the young date palm roots are located. This determines the temperature of the soil moisture and must largely govern the temperature of the ascending sap current.

In Indio the soil temperature at 2 feet deep is surprisingly constant, the diurnal range during the period of the experiment not exceeding 0.5°, and during the heat of the summer not exceeding 1° to 1.5° F.

The relatively low temperature of the Indio soil can be attributed in part to its peculiar physical character. The deeper strata are composed of the old lake bed silts, above which are alternating layers of fine silts from the widely dispersed shallow flooding from the Whitewater River and wind-blown fine sand with a high proportion of fine particles of mica. It has a high water capacity without the danger of becoming "puddled" or impervious to air as does a clay soil with repeated wetting.

The ample irrigation practiced at this garden doubtless is largely responsible for the soil being retained at a moderate temperature. The mean air temperature for June, July, and August, 1918, was 91°. The temperature of the water from the artesian wells used in irrigation is about 74°. With an irrigation every 10 to 14 days, the cooling effect of this volume of water, with the added cooling of evaporation would result in keeping the soil temperature several degrees below the mean air temperature of the hottest weather. Free (*7*, *p. 188*) attaches much importance to the high specific heat of soil water. From his statements we may conclude that the retarded warming up of the soil due to water, a disadvantage in the spring on an eastern farm,

becomes a positive advantage under the extreme heat of a desert summer. The seasonal range of soil temperature at the Indio garden at the depth of 2 feet is a narrow one, extending in 1918 from 57° in January to 85.5° in August, an amplitude of only 28.5°. For comparison, soil temperature studies by Bouyoucos at the Michigan Agricultural Experiment Station in 1913 (*1, p. 63, 68*) may be quoted, showing in loam soil at 18 inches deep a minimum temperature of 31.3° in February, and a maximum of 76.9° in July, giving a yearly amplitude of 45.6°. The Indio date garden soil temperature at 2 feet declined from 58° on February 18 to 57° on February 21, then slowly advanced to 67° by March 31 and to 71.5° on May 4 (the time covered in Tables I to V).

INFLUENCE OF THE ASCENDING SAP CURRENTS

In the records from February 18 to 21, Table I, also from March 9 to 15, and again from March 19 to 21, the position of the daily air mean below the soil temperature, and the close correspondence of the tree temperature with that of the soil point unquestionably to the sap current as a controlling temperature factor.

Most significant is the record of the morning of February 19 (Table I and fig. 5), when there was a sharp frost, with an air temperature of 26.6° F. beside the tree (standard minimum in Weather Bureau shelter, a few hundred yards distant, 25°). At 6.30 a. m. the tree record was 55.4°, which slowly declined to 52.7° between 9 a. m. and 10.30 a. m., then ascended in the afternoon to 55.4°.

The thermograph trace kept near the tree shows that the air temperature was below the freezing point for 5 hours, from 2.15 to 6.45 a. m., so we must conclude that the freezing temperature produced its greatest depressing effect on the interior tissues of the bud only after a lag of from 7 to 8 hours. The lower thermometer in the trunk did not reach its minimum of 56.3° until 2.30 p. m., showing here, as do the subsequent records, that the trunk tissues are less sensitive to the air temperatures than those of the bud.

With the thermometer in the bud zone showing a drop to only 5.3° below the soil temperature of 58°, and the lower or trunk thermometer indicating only 2° below the soil temperature, it is evident that the ascending sap current must have been the controlling factor, protected from air temperature by the insulating outer layers. Although the movement of the ascending sap current due to transpiration is reduced to its minimum at this part of the 24 hours, the large volume of water in the trunk and bud has a specific heat about five times greater than that of the solid soil particles. This offers to the outside cooling influence a resistance which is of the utmost importance to the tender tissues at this critical period.

During this frost period of February 19 both tree thermometers registered temperatures safely above 50°, which temperature the writer has found to be the minimum point for growth of the date palm leaves (*17*).

A sharp decline in the growth rate of the leaves of this tree for both February 19 and February 20 indicates that the zero point of this rather sensitive variety had been closely approached; yet the growth of 1.5 2 mm. on February 20 shows that the actual zero point, as applied to growing tissue, had not been reached with the

interior temperature at 52.7°. This is an example of the importance in growth-temperature studies of knowing the actual temperature maintained within the growth-center, although such knowledge is usually difficult to obtain.

Another conclusive proof that the lower curves of the interior temperatures are in large measure due to the cooling influence of the ascending sap current lies in the records of April 21 to 27 (Table IV and fig. 6) where on the 23d, 26th, and 27th particularly, the midday temperature shown by the lower trunk thermometer was 3° to 5° lower than that of the upper one and on the latter date actually coincided with the soil temperature. While the retarded effect of the cool night air has an undoubted influence in bringing about the lowered temperature of the interior at midday, the records of February 19 show that the interior of the palm at the growth center is much more sensitive, and more quickly reacts to external cold than does the trunk interior near the ground. Affected only by the cooling of the night air, then, the upper thermometer, after allowing time for the lag, should show a lower midday temperature than the thermometer 2 feet from the ground. This has occurred only a few times; once on February 19 under the influence of the sudden drop to 25°, which was more than sufficient to overcome the influence of the soil water at 58°.

The influence that could keep the lower trunk center at a lower temperature than the upper one at midday would be that of the ascending sap current, which would be most active during the period of greatest transpiration. Although the growth-center temperature is no doubt lowered by the same influence, the ascending sap reaches it later, after having absorbed more heat from the surrounding tissues. Though no observations have been made on the hourly transpiration rate of the date palm, the studies of Briggs and Shantz at Akron, Colo. (*3*), show that for a variety of plants, but especially wheat and rye, the maximum of the day's transpiration occurs later than midday, often between 2 and 3 p. m. It will be noted from the Tables I to VI of interior temperatures of the date palm that the minimum recorded by both the upper and the lower thermometers is usually at a point about midway between 12 noon and 6 p. m.

April and May, being unusually cool, did not afford the usual examples of high temperatures, but April 29 and 30 and May 1, 2, and 3 gave maximum air temperatures of from 95° to 99.5° F. with daily means from 78.5° to 82.5° (Table V). Yet the minimum interior temperature of the Zaheedy tree by the lower thermometer at 3 p. m. (the upper one was broken) was 71.6° on the 29th and 72.5° on the 30th, with the soil at 70° and 71°. During the first three days of May, with air maxima reaching 98° and 99.5°, this interior temperature was only 2.5° to 2.7° above that of the soil. On May 2, with the maximum air temperature 99.5°, the interior of the Zaheedy touched a minimum of 73.4°, a protective cooling of 26.1°. At the same time the growth center of the Maktoom tree gave a minimum of 76.1°, giving these active cells a cooling effect of 23.4° below the air maximum. For this entire period the temperature curve for the lower Zaheedy thermometer was below the daily mean air temperature. With two exceptions, the growth center temperature of the Maktoom was also below it. This gives another proof of the cooling influence of the ascending sap current.

Here, again, the principle of the high specific heat of water plays a most important part, conversely to that when air temperatures are below soil temperature; water is slow to cool or give up its heat, but is also slow to absorb it, hence serving as the great factor in stabilizing temperatures of the tissues of the growth center.

A LATER SERIES OF RECORDS

The most convincing proof that the temperature of the soil water is the chief governing factor in regulating the interior temperature of the trunk during hot weather is found in records secured in the spring of 1923 by the study of a large male palm known as the "Mosque Male" in the collection at the Indio date garden. This tree was a 9-year-old seedling at the time and 11 feet high to the top of the bud, with a trunk diameter of 2 feet at 4 feet high. Doubtless the greater size and more mature age of this tree rendered it less susceptible to changes in air temperature than the smaller trees of the earlier tests, also the greater extent and deeper penetration of its roots would give a different reacton in relation to soil temperatures. In February a thermometer was placed in the trunk at 4 feet high, the bulb reaching to the center of the tree, and another in the near-by soil 2 feet deep. It was not expedient to place a thermometer in the growth center of this valuable tree.

The records obtained showed that the trunk temperatures were higher than those of the soil by 2° to 4° F. in the early morning, but approached most closely at about 2 to 3 p. m., occasionally coinciding. On May 5, a very hot day, the first of the season, trunk temperatures from 10 a. m. to 4 p. m. were lower by 1° to 1.75° than the soil temperatures at 2 feet deep. On May 7 another soil thermometer was installed at a depth of 3 feet.

It at once became clear that the lower trunk temperatures were due to soil water drawn from a greater depth than the 2-foot layer. Table VI, for May 5 to May 11, comprises a period of unusually high temperatures for the early part of May with the air of desert dryness, according to Indio date garden records, the relative humidity at 2 or 3 p. m. being only 10 to 15 per cent.

The trunk temperatures declined from about 8 a. m. until 2.30 or 3 p. m., the period when leaf transpiration is presumably the greatest. Here the trunk temperature fell below that of the soil at 2 feet, and at times approached closely to that of the soil at 3 feet, where the heavier feeding roots of a tree of this age are found. Evidently the heavy demand made upon the roots for water at the mid-afternoon period carried the sap up through the trunk at such a rate that there was comparatively little lowering of the temperature at which it left the soil. At what actual temperature this sap reached the growth area of the bud, 5 or 6 feet higher, must be inferred from the records obtained in 1918 from smaller trees. Table IV shows that when the soil temperature at 2 feet was 71° F., the midday temperature in the growth area was 3° to 5° higher. A 6° increase in sap temperature for the Mosque Male (from soil at 2 feet to the growth area of the bud) would give this region a temperature around 80° at the time when the air maximum was 108° to 110°, or a protective temperature difference of from 28° to 30°. It must be remembered that the basal growing points of all incompleted leaves (of which there may be 6 or 8 in process of elongation at once) center in this

area of cell division. A fruiting tree has in addition the bases of 6 to even 15 fruit-bearing stalks which continue their elongation well into the summer; also, the nourishing of the rapidly growing bunches of fruit must be provided for. The work performed in this huge growth center is therefore very great and the temperature protection afforded by the ascending sap current during the intense heat of the desert afternoon is of the greatest importance.

While attributing a most important influence to factor (*3*), the ascending sap current, it is evident that that can only be effective within the protecting and insulating influence of the protecting envelope and the fibrous outer tissues of the trunk proper.

Without these the sap current would be brought to the air temperature before it could reach the growth center. It might be compared to the attempt to convey hot water or steam from a heating boiler to a radiator in a distant building without the insulating coverings and inclosed conduits which heat engineers provide for such service.

Unusual space is given to this topic because in the idea of the regulating value of the ascending sap current in determining the temperature of the phyllophore of the palm there appears to be a heretofore unrecognized principle in plant physiology, of first importance in the date palm, the Washingtonia, and other desert endogenous plants, and not to be ignored in the economy of exogenous plants, both woody and herbaceous.

DISCUSSION

EQUALIZATION OF TEMPERATURE IN THE GROWTH CENTER BY TISSUE INSULATION

The idea of the thermos bottle preserving the temperature of either cool or hot contents was anticipated by the date and other palms, though unrecognized all these years. In fact this idea clearly explains the wonderful adaptation of such palms to the extreme temperature ranges of their environments. The heavy layer of fiber surrounding the trunk of the date palm is only relatively less efficient than the arrangement of outer and inner flasks with a nonconducting vacuum zone between. The excessive heat of the midday air and the chill of the frosty night alike penetrate but slowly toward the tender embryonic cells in the bud. The strong volume of the sap current, absorbed by the roots at deep soil temperatures, ascending through the intricate vascular system of the trunk, is able to preserve most of its low temperature until it is dispersed in the leaves, because of the low conductivity of the protective envelope, the layers between it and the surrounding air. Thus the stabilization of temperature in the growth center of the date palm is established.

It is not too much to affirm that but for this protective adaptation to the extreme heat conditions of its environment, the death point for the growing tissue of the date palm would be reached nearly every year in the Sahara, and frequently in its adopted home in southern California. This would hold equally true of the Washingtonia, the one native palm of California, in which the writer has observed temperature differences between the growth center and the air similar to those of the date palm. The survival and majestic growth of the Canary Island palm, *P. canariensis*, at the Furnace Creek Ranch in the Death Valley of California, with almost the world's highest heat record, can be explained on no other hypothesis.

THE TEMPERATURE OF RESPIRATION

Without means for definite determination, it must nevertheless be assumed that to the warming effect of the daily air maxima there should be added some amount of heat developed by the activity of the enormous bud, which comprises not only the region where new organs are in formation but also the basal zones of all leaves still in process of elongation, sometimes six or eight in number. Jost (*9, p. 398–401*) mentions "growing points" along with germinating seeds and inflorescences as exhibiting temperatures higher than that of the surrounding air, but lays special emphasis on the high temperatures observed in the inflorescences of Palmeae, Cycadaceae, *Victoria regia*, and *Arum italicum*. He adds in the supplement (*10*): "The heat produced is thus not a protection against frost."

MacDougal (*14, p. 57*) by inserting thin-bulbed thermometers "in the tissues of joints of cacti from which new shoots were arising" observed temperatures at times 8° or 9° C. above surrounding air. The writer is unable to find any record of such temperature tests of the buds or growth centers of palm trees. Of the comparative temperatures illustrated in the five figures previously referred to, the greatest actual difference between the growth center and the surrounding air was 28.8° F. at 6.10 a. m. on February 19 (Table I). For protection to the growing tissue this was most important, since in the adjacent garden buds of many deciduous fruit trees were destroyed by that freeze. This was at a time when the night leaf growth was only 3 mm., hence the cell activity and respiration must have been very slight and the generation of heat from this source negligible.

The extent to which respiration becomes a factor in the interior temperature of the phyllophore may well be left to further experimentation.

It has been shown in another line of experiments that the leaf elongation of the date palm is made in the night and that growth entirely ceases in direct sunlight. But it has also been demonstrated that by excluding all light from a date plant at midday, a rate of growth is quickly resumed similar to that of the night hours. This would involve the activity of the meristem cells of the growth center following a maximum of respiration. Any rise in temperature, contrary to the usual downward direction of the temperature curve at this hour, could then be credited directly to the respiration in progress.

With the aid of a recording auxanometer and a recording resistance thermometer, it should be possible to coordinate almost to a minute the resumption of the suspended growth with any rise in temperature.

TEMPERATURE CONTROL OF THE GROWTH CENTER OF ENDOGENS

A survey of the literature on the temperature relations of plants fails to show recognition of the following four vital facts of plant physiology which are brought out in these studies of the date palm:

(1) The existence in an important plant group of what may be termed "giant buds" or growth centers, within which are in progress simultaneously (and in the date palm, at least, perennially) the basal or intercalary growth of leaves and flower spathes, and the apical growth of the trunk.

(2) Stabilized temperatures within this growth center, with a decided gradient between them and those of the surrounding air, higher or lower, as the case may be.

(3) An insulating zone of tissues of low conductivity, surrounding the growth center, and resisting the penetration of air temperatures from without and the escape of heat from within; a stabilizer.

(4) The stabilizing influence of the ascending sap current, tending to hold the growth center temperatures within a few degrees of the temperatures of the soil penetrated by the plant roots.

Pfeffer (*19, pp. 379, 381*) appears to have had an understanding of the influence of the ascending sap current in exogenous trees.

Rameaux (*20*) recognized the influence of "organic action" as "vital heat" in the plant, but attributed the plant temperature chiefly to "the influence of the climate, acting in two different manners—(1) directly upon the plant organs exposed to the atmosphere; (2) upon the soil and consequently upon the sap drawn up by the plants."

The direct action of the sun's rays was considered the strongest influence in governing plant temperatures and he recognized the effect of the slow penetration of the heat through the badly conducting wood.

Thus the alternations of the day's heat and the night's coolness did not reach the center of the trunk of 0.5 meter diameter until after a lag of 15 hours, or even 24 hours.

However, with the exogenous trees which were under observation, such temperature phenomena could have had little stabilizing influence on the meristematic tissues and none is claimed by this author; for he records that "during the warmest days of April, a branch of a poplar, 4 cm. thick, showed in the central strata a temperature at noon which was 8°, 10°, or even 13° C. higher than the surrounding temperature."

Of the influence of the sap current, Rameaux says: "The ascending sap increases or diminishes the temperature of the parts which it traverses according as these parts possess a temperature lower or higher than that of the sap itself."

Much importance is attached by this author to the transpiration rate of the foliage in enhancing the flow of sap through the trunk and branches and so increasing its cooling power as it meets the heat penetrating from the surface. In support of this idea he submits a table of the interior temperatures recorded in two trees; in the first period, growing normally, the temperatures of the two trees during various hours of the day compared very closely. During the second period, with the second tree dead and presumably not transpiring and without the ascending sap current, the dead tree showed during the afternoon temperatures of from 7° to 10° higher than those of the normal tree cooled by the ascending sap. In the third period, with tree No. 1 shorn of all its top, hence with no ascending sap current, its interior temperature compared closely with that of the dead tree.

DeCandolle (A. P.)[7] (*6*) Physiologie Végétale, is cited frequently by both Pfeffer and Rameaux. DeCandolle recognized the impor-

[7] Citations from DeCandolle, Aug. Pyr., (*6*) in Physiologie Végétale; (p. 879) Schoepff (*2*) *Naturforscher*, 23 sti., p. 1–37. Halle, 1788; (p. 880) Hermstaedt (*2*), *Mag. d. Gesellsch. naturf. freunde in Berlin*, 1808, p. 316; (p. 879) J. Hunter, (*1*) *Philos. trans. for* 1775 et 1778; Journ. de phys., 9, p. 294; 18, p. 12 et 216.

tance of the ascending sap current in regulating the temperature of the trunk interior and stated that "Buffon was the first author to observe that when we cut trees in the winter, the interior part of the trunk appears to be warm, especially close to the center, * * *."

He cites Hunter (p. 879) as the first to try to explain the phenomena by placing a thermometer in a hole bored in the trunk of a large walnut tree, where he obtained in autumn, temperatures 2 or 3 degree above the surroundings. He was followed by Schoepff of New York (p. 879) and Bierkander of Sweden, confirming the earlier work.

DeCandolle cited John Schöpf (*21*), who published "Ueber die Temperatur der Pflanzen," in Naturforscher, Halle, 1788. This is a record of observations made at New York in 1783 on the temperatures within the trunks of several species of trees, black, red and white oak, wild cherry, chestnut, and beech, compared with those of the surrounding air. He observed distinct gradients between tree and air temperatures, notably one morning with the air at 22° at 7.45, when the interior of a 3-foot chestnut showed 36°. Schöpf is quoted as having "repeated and enlarged" Hunter's experiments. These records, probably the beginning of the study of plant physiology in the United States, he interpreted as proving that plants generated in themselves a vital heat analogous to that of warm-blooded animals. He failed to associate the higher interior tree temperatures with the ascending sap current and soil temperatures.

DeCandolle further records that Pictit and Maurice at Geneva, by the use of several thermometers, some in the trunk of a large chestnut tree, others in the soil at various depths, arrived at a true solution of the problem:

> They noticed that the variations in the internal temperature (in the trunk) corresponded plainly with the temperature given by the thermometer placed in the soil at the depth of 4 feet, thus in the vicinity of the roots of the tree.

Hermstaedt (p. 880) is quoted as observing a temperature of plus 1° R. (34.25° F.) within a tree when the air temperature was minus 10° R. (9.25° F.). DeCandolle sums up this part of the problem as follows:

> In bringing these facts together, and especially the last ones mentioned, Rumford's theory about the ascension of the sap helps us to appreciate the problem dealing with the internal temperature of plants as I have attempted to explain in 1805 in the "Principes de Botanique" in the introduction to the Flore Française. * * *
>
> The water absorbed by the roots ascends vertically in the trunk. This water shows the temperature of the soil at the middle depth of the tree roots; it is consequently warmer than the atmosphere in the winter and cooler in the summer.

The insulating effect of the bark and the outer layers of the trunk in conserving the heat of the ascending sap is recognized in the following paragraph:

> Therefore, while the ascension of the sap tends continually to bring the temperature of the center of the trunk to an equilibrium with that of the soil, the whole structure of the woody body of the trunk and especially that of the bark, prevents the temperature from reaching an equilibrium with the surrounding air.

A summary of these observations on the interior temperatures of trees, dating back from DeCandolle in 1832 to Schöpf in 1783, and Hunter in 1775 shows the following points generally accepted:

(1) The paramount influence of the air temperature and, in sunlight, the sun's rays incident upon the surface of the trunk and branches, in controlling the interior temperature of the tree.

(2) Balanced against the first, the influence of the ascending sap current, deriving its temperature from the soil at the depth of the greater mass of the absorbing roots, hence subject to but moderate fluctuations. It was recognized that this sap current might exert a cooling or a warming influence on the general body temperature of the plant according to whether it was of a lower or higher temperature than that derived from the air; becoming a cooling influence in the summer, a warming one in the winter.

(3) Interposed between the external air and the trunk interior, DeCandolle recognized the insulating value of the bark and the woody trunk, resiting the penetration of the exterior heat or cold on the one hand; blanketing and conserving the temperature of the ascending sap on the other.

(4) The importance of leaf transpiration in inducing the flow of the sap current was recognized when the top was removed from the tree in Rameaux's experiment, the rise of the trunk temperature when exposed to the sun being attributed to the absence of the cooling sap current ascending at soil temperature.

Influence of the interior temperature on the growth centers and cambium is nowhere suggested, nor was there any recognition of the giant buds which characterized such genera as palms, yuccas and Dracenas, nor of the specially insulating layers which surround such buds in the date palm.

LIMITATION OF THE GEOGRAPHICAL RANGE OF THE DATE PALM BY TEMPERATURE

The geographical occurrence of the date palm must be considered under two categories.

(1) THE ARTIFICIAL OR PLANTING RANGE

The artificial or planting range in which the date palm will survive is a much wider one than the range of fertile seed production and must be limited by such a degree and duration of cold as would enable frost to reach the meristematic tissues of the growth center. It has been shown in previous pages that growth was not wholly checked by minimum temperatures above 21° or 22° F. of short duration, but many hundreds of palms in the Coachella Valley of California survived minimum temperatures of 13° to 15° January 7 and 8, 1913, with only a severe killing of the leaves. At the United States Experiment Station at Sacaton, Ariz., this same cold spell gave minimum temperatures, January 6, 9°; January 7, 10°; and January 8, 11°; with similar results, a severe freezing of leaves, but the growth center unharmed. In San Antonio, Tex., previously referred to, mature palms have survived minimum temperatures of 4°, though all foliage was killed. The short duration of the severe cold would have had little effect on the soil temperature penetrated by the roots and the latent heat of the sluggish sap current must have been able to overcome the penetration of cold toward the bud.

(2) THE NATURAL OR SEED PRODUCTION RANGE

The natural or seed production range of the date palm would be within a climatic area which would permit the production of viable seeds for the propagation of the species. This lies far inside the area

where the palm may survive if planted. There are limits to the laying down of the flower spathes, which would be governed by the temperature maintained in the phyllophore during the season of greatest heat. This would probably involve also a certain optimum intensity of the sun's rays, governed both by the angle of incidence and by the amount of watery vapor intervening, for the relation between photosynthesis and growth in the date palm is to a great degree a daily and direct one instead of the seasonal one that it is largely in exogenous trees. But throughout, the temperature of the sap current, under the insulation of protective layers of fiber, will be found as regulatory as a thermostat.

DUAL TEMPERATURE REQUIREMENTS OF THE DATE PALM

Thus the date palm has two very distinct temperature requirements. The first is effective insulation and protection of the tissues, while in the embryonic stage, against extremes of heat and cold. The second is high temperatures from both the surrounding air and the radiant heat of intense sunshine for the promotion of photosynthesis and the building up of a fruit crop with a high sugar content.

SUMMARY

The date palm is the most resistant to extremes of heat and cold of any member of the palm family. As a species it has survived without permanent injury extremes of temperature from 4° to 125° F. This wide range of adaptability is believed to be largely due to the morphological structure and physiological action outlined in the following paragraphs:

The date palm, along with other members of the palm family, has its active growing tissue centralized in a giant terminal bud or phyllophore from which are in progress simultaneously the basipital or intercalary growth of leaves and flower spathes and the elongation of the trunk and its thickening to the established diameter.

Within favorable temperature limits, and with sufficient water supply, the growth of the date palm is continuous throughout the year, the curve of mean daily leaf elongation being closely parallel to the curve of mean daily temperature. Growth may be continued when the minimum air temperature of the day is several degrees below the freezing point, provided the maximum temperature of the day is well above the growth zero point, 50° F.

Thermometers inserted in date palm growth centers show a stabilizing of temperatures with a marked gradient between them and those of the surrounding air, but with a striking correspondence with the temperatures of the soil strata penetrated by the palm roots.

The daily range of these interior temperatures is slight and rarely exceed 7 or 8°, but with an inverted curve, relative to the air temperature curve, highest at about sunrise, lowest at from 2 to 4 p. m.

The difference of the interior temperature from the surrounding air has ranged from 26° warmer on the coldest morning observed, to 32° cooler on the hottest day.

This protective stabilizing of the temperatures of the meristematic tissues of the date palm is believed to be due to two principal factors:

(1) *A protective envelope surrounding the growth center*, of a highly nonconducting and insulating nature, composed of the thick, fibrous,

overlapping leaf bases, with the accompanying fibrous sheath and lower down the outer zone of the trunk proper. Through these layers the air temperatures, cold or hot, penetrate very slowly and with considerable loss.

(2) *The ascending sap current*, with a temperature acquired from the soil from which it is drawn by the roots. Under the insulation afforded by the protective layer and the outer portions of the trunk, the sap is able to reach the growth center at a temperature varying but a few degrees from that at which it left the soil, and so is able to neutralize much of either cold or heat, as the case may be, that has penetrated from without.

It is believed that in the discovery of this stabilizing of the temperature of the growth center of the date palm is disclosed a principle heretofore unrecognized in plant physiology, and one of vital importance to palms and other endogenous plants in desert environments in enabling them to survive the extremes of their temperature exposures.

LITERATURE CITED

(1) Bouyoucos, G. J.
1916. soil temperature. Mich. Agr. Exp. Sta. Tech. Bul. 26, 133 p.

(2) Branner, J. C.
1884. the course and growth of the fibro-vascular bundles in palms. Proc. Amer. Phil. Soc. 21: 459–483, illus.

(3) Briggs, L. J., and Shantz, H. L.
1916. hourly transpiration rate on clear days as determined by cyclic environmental factors. Jour. Agr. Research 5: 583–650, illus.

(4) Brown, T. W.
1915. the date palm in egypt. part 1. Agr. Jour. Egypt 5: 63–79, illus.

(5) Candolle, Alph. de
1855. géographie botanique raisonnée. t. 1. Paris.

(6) Candolle, Aug.-Pyr. de
1832. physiologie végétale. t. 2. Paris.

(7) Free, E. E.
1911. studies in soil physics. v. soil temperature. Plant World 14: 186–190.

(8) Gourley, J. H.
1917. some observations on the growth of apple trees. N. H. Agr. Exp. Sta. Tech. Bul. 12, 38 p., illus.

(9) Jost, L.
1907. lectures on plant physiology. Tr. by R. J. H. Gibson. 564 p., illus. Oxford.

(10) ———
1913. plant physiology. Translated by R. J. H. Gibson. Supplement incorporating the alterations of the second edition of the German original. 168 p., illus. Oxford.

(11) Lehenbauer, P. A.
1914. growth of maize seedlings in relation to temperature. Physiol. Researches 1: 247–288.

(12) Livingston, B. E.
1916. physiological temperature indices for the study of plant growth in relation to climatic conditions. Physiol. Researches 1: 399–420.

(13) ——— and Free, E. E.
1917. the effect of deficient soil oxygen on the roots of higher plants. Johns Hopkins Univ. Circ. (n. s. 3) 293: 182–185.

(14) MacDougal, D. T.
1917. temperature and growth. Carnegie Inst. Wash. Yearbook (1916) 15: 55–57.

(15) Martius, C. F. P. de
[1850]. historia naturalis palmarum. v. 1, illus. Lipsiae.

(16) MASON, S. C.
1915. DATES OF EGYPT AND THE SUDAN. U. S. Dept. Agr. Bul. 271, 40 p., illus.

(17) ———
1925. THE MINIMUM TEMPERATURE FOR GROWTH OF THE DATE PALM AND THE ABSENCE OF A RESTING PERIOD. Jour. Agr. Research. 31: 401–414, illus.

(18) MIRBEL, [C. F. B.] DE
1843. PHYSIOLOGIE VÉGÉTALE.—RECHERCHES ANATOMIQUES ET PHYSIOLOGIQUES SUR QUELQUES VÉGÉTAUX MONOCOTYLÉS. (PREMIER MÉMOIRE.) LE DATTIER (PHOENIX DACTYLIFERA). Compt. Rend. Acad. Sci. [Paris] 16: 1213–1235.

(19) PFEFFER, W.
1906. THE PHYSIOLOGY OF PLANTS. Ed. 2. Translated by A. J. Ewart. v. 3, illus. Oxford.

(20) RAMEAUX.
1843. DES TEMPÉRATURES VÉGÉTALES. Ann. Sci. Nat., Bot. (sér. 2) 19: 5–35.

(21) SCHÖPF, J. D. (SCHOEPFF, J. D.)
1788. UEBER DIE TEMPERATUR DER PFLANZEN. Naturforscher [Halle] 23: 1–36.

(22) SHREVE, F.
1911. THE INFLUENCE OF LOW TEMPERATURES ON THE DISTRIBUTION OF THE GIANT CACTUS. Plant World 14: 136–146, illus.

(23) SMITH, A. M.
1906. ON THE APPLICATION OF THE THEORY OF LIMITING FACTORS TO MEASUREMENTS AND OBSERVATIONS OF GROWTH IN CEYLON. Ann. Roy. Bot. Gard. Peradeniya 3: 303–374, illus.

(24) VINSON, A. E.
1914. THE EFFECT OF CLIMATIC CONDITIONS ON THE RATE OF GROWTH OF DATE PALMS. Bot. Gaz. 57: 324–327, illus.

THE INHIBITIVE EFFECT OF DIRECT SUNLIGHT ON THE GROWTH OF THE DATE PALM[1]

By SILAS C. MASON

Horticulturist, Office of Crop Physiology and Breeding Investigations, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

A study of the habits of the growth of the date palm reveals an adaptation to the conditions of desert climates to which attention has only recently been directed (*5, p. 3, 4*).[2]

The lower minimum temperature point for growth has been treated (*6*), leaving still much work to be done on the optimum and maximum cardinal points for growth. The protective temperature regulation of the growth center and its influence on other temperature reactions, making growth possible the whole year, has been shown (*7*). The reaction of the date palm and a number of other palm genera to light conditions are considered in the present paper.

The date palm, along with many other palms, has a diurnal period of leaf elongation, in darkness or in the absence of direct sunlight, alternating with a complete cessation of growth in bright sunlight. This diurnal alternation of growth and rest, occurring inversely to the exposure to direct sunlight, is discussed in the following pages.

The literature on the growth habits of the date palm is very meager and the most of it is lacking in definiteness. Branner (*1, p. 481*) states:

> In conclusion I find: (1) That all fronds and spadices originate at the center of the phylophore; (2) that the fibrovascular bundle division continues to grow until its frond reaches maturity; (3) that the growth of a palm trunk continues as long as the bundle divisions of the part are in active connection with living fronds, and no longer; and (4) that the growth of palms is therefore an internal growth, and the term "endogen" is not a misnomer as far as palms are concerned.

The inference that the entire growth of the leaf is made within the "phylophore" (correctly phyllophore) may be drawn from this, but is not positively stated.

A study of date-palm growth involves the questions: (1) In what regions of the plant is the growth made? (2) What relation does growth bear to temperature? and (3) What relation does growth bear to light and darkness?

The experimental approach to these questions calls for methods adapted to the particular structure of the date palm which is distinct from exogenous plants generally and also from many other genera of palms.

TERMINAL LEAF GROUPS

The leaves of the date palm when full grown are distributed around the axis very accurately according to the system of phyllotaxy of the genus; but in emergence from the bud they appear to follow growth impulses or waves in that from three to five leaves emerge together in close contact and with the perfectly formed

[1] Received for publication Sept. 26, 1924; issued October, 1925.
[2] Reference is made by number (italic) to "Literature cited," p. 468.

pinnae closely appressed, maintaining a growth rate as one individual. The form suggests an acutely sharpened stake for which the writer proposes the name *palus*, from the Latin *pālus*, a stake.

This palus or synchronous group of leaves may be extruded to a length of 2 or 3 feet before the new growth from within separates them and they assume an individual rate of elongation.

EXPERIMENTAL DATA

METHODS OF THE EXPERIMENT

In order to determine the various questions of growth in relation to light and temperature, seven seedling trees at the United States Date Garden at Indio, Calif., were selected for observation.

As the palus of new leaves emerged from the buds of two of these selected individual leaves were marked into 1 cm. and 10 cm. divisions, in order to learn whether any further elongation was made. The length of unexpanded pinnae was also recorded to learn whether they had attained their full length. In no case was any further elongation of light-exposed portions of either rachis or pinnae observed. A varying portion of the leaf was pushed up daily from the heart of the bud, the movement of which will be discussed later. The depth at which actual elongation of the tissue was taking place could only be surmised from external observations.

Next a discarded male tree about 5 years old was dissected in order to trace the elongation to its source. A sector of one-third of the circumference was cut out to 10 inches below the top of the bud, and two-thirds of the radius toward the center. Without invading the very center of the bud, portions of the bases of several of the younger leaves were reached where the tissue was ivory white, the fibrovascular bundles yet unhardened, and the whole substance easily broken with a square brittle fracture. While these dissections were being made, the admirable binding quality of the fibrous older sheaths was at once apparent. The whole central part of the bud was in a state of tension from the turgescence of the growing parts within. A distinct popping sound could be heard as the tensely strained layer of "leef" or sheath fiber was severed with a quick cut of the knife and the pressure within relieved. If the leaves in the bases of which lignification had not taken place were not supported at once, they were broken by the slightest swaying by the wind or overbalanced by their own weight. Ten-centimeter portions were marked in centimeters on the succulent exposed portions of five such leaves, and these again marked in millimeters with a needle point.

Here, finally, proof of elongation was secured. The millimeter spaces in the lower portion of the marked areas were found to be farther apart in the daily observations, though the elongation was slight and continued only three days. The slight pushing up of the leaf from below showed that only the upper portion of the elongating area had been exposed. It seems probable that exposure to the air checked the elongation after three days, and that the severe cutting brought the whole growth to nearly the zero point. Subsequent experiments, where holes were bored to the center of the trunk, determined that this pushing up of tissues was quite active 18 inches below the bud crown, and at 2 feet below there was still a discernible action. This mode of growth is referred to as "basipetal" by Jost in the following paragraph: (4)

Frequently we meet with another type of leaf expansion where the apex at once passes into a state of rest. This is the case in many lianes where specially formed apices, fulfilling particular functions, are produced long before the rest of the lamina is completed. The elongation is basipetal also in the long leaves of monocotyledons, owing to the development of an intercalary growing zone at their bases.

Attention has been called (7) to the fact that all of this basipetal growth was so deeply seated in the bud as to be in complete darkness; quite the reverse of the mode of terminal growth of endogenous shoots like the bamboo or in the twigs of exogenous shoots like the apple or the pine, where cell division must go on within translucent tissue, or in very small twigs in nearly full sunlight.

PERIODICITY OF LEAF ELONGATION

Several trees of different ages were selected for study of their leaf growth, five of the newest central leaves being designated by letters, and the trees by their place numbers in the blocks.

The method of recording the advance in growth was by driving stakes, or for taller trees by erecting little towers. Upon these were placed carefully leveled crosspieces, over which a steel square enabled the record marks to be made on the ribs of the leaves with a thin-bladed knife. A day's growth of as little as 1 mm. could be accurately recorded. At first observations were made morning and evening, but the fact was soon disclosed that with occasional exceptions the expansion or pushing up from below took place almost wholly at night.

As it was not feasible at first to keep these records in close coordination with sunrise and sunset, the observations being made about 8 a. m. and 4 p. m., only the general facts of the relation of growth to light and darkness were brought out. Two facts, however, soon gained prominence, in addition to the main one (that the chief growth is made in darkness). The first was that intermittently some growth was made during daylight hours. Whether this was a holding over or prolongation of the night growth, or was due to conditions occurring during the day, could be shown only by securing continuous or auxanometer records. The second fact noted was that certain leaves, and on some days several of them, were actually shorter at night than when the morning reading was made. This interesting phenomenon, which has been observed in the growth history of a variety of plants and is attributed to decreased turgescence of the cells, will be made the subject of further study.

AUXANOMETER DATA

In April, 1918, an auxanometer was installed by making use of an anemometer clock having a horizontal recording cylinder revolving once in six hours. The spirally threaded spindle for carrying the record cylinder laterally to receive the wind velocity record was discarded, leaving the cylinder its rotary motion in a fixed position on its axis, and a pen-carriage was constructed to move from left to right at the pull of the wire actuated by the leaf growth. This clock in its case, was placed on a rigid stand by the side of the tree to be observed.

Since the midrib of the date leaf was quite rigid and pushed upward by a positive expansion below in the heart of the bud, an

upward pull on the fine piano wire fastened to the rib a few inches from its emergence from the bud gave a direct index of the growth being made. A piece of coiled wire tubing fastened rigidly to the palm trunk below the record leaf and to the side of the clock case served as a conduit for the piano wire between its attachments to the leaf and to the pen-carriage. The pen-carriage traveled on two parallel horizontal guide rods, and the beginning of a record was placed at the left hand or distal end of the cylinder. The pull of the wire to the right in response to the growth was counterpoised by a small rubber band on the left, giving a positive and steady motion to the pen. At the same time the position of the band was adjusted to regulate the pen pressure on the record cylinder.

Although this mechanism develops some friction on the wire, and is lacking in the extreme delicacy usually essential to an auxanometer, the strong up-push of the growing date leaf and the rigidity of the rib probably compensated for these features; and the general stability of this device was a positive advantage in out-of-door conditions, with almost constant high winds to be withstood. It is obvious that with this arrangement the pen traces a smooth line around the cylinder and parallel with the base when no growth is made, while growth is recorded by a slowly advancing spiral. As the circumference of the

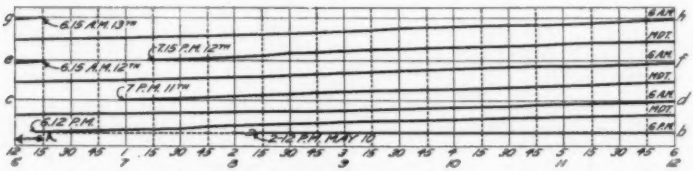


FIG. 1.—Auxanometer record of growth of date-palm leaf at the Government Date Garden, Indio, Calif., May, 1918

cylinder, making one revolution in six hours, is 12 inches, the cylinder must rotate past the pen one-sixth of 12 inches or 2 inches in one hour. Hence each five-minute period would be represented by one-twelfth of 2 inches or one-sixth of an inch on the circumference of the cylinder; while the longitudinal progress of the pen on the cylinder, actuated by the pull on the piano wire, would record the actual growth made.

This secures a fairly accurate recording of the beginning and ending of the growth periods, as well as a comparison of the growth rate during the different periods of the night.

When no day growth is made the pen does not advance and the pen-trace runs around the cylinder as a single line parallel to the cylinder heads at the point where growth ceased.

Between sunrise, when growth ceases, and sunset, when growth is resumed, the cylinder would make nearly two complete revolutions with the pen tracing the same mark.

Table I shows the daily growth, in millimeters, before and after midnight, with the time of beginning and ending from April 24 to May 20, inclusive. Figure 1 reproduces a tracing from one of the record sheets, most typical of three days' growth. (One should imagine this wrapped around the cylinder, with *c* and *d* contiguous and revolving in the direction of the arrow *A*.)

The horizontal lines *c–d*, *e–f*, and *g–h* show two revolutions of the drum during sunlight without registering growth. The heavy lines

ascending from left to right show night growth beginning at 6.12 p. m., 7 p. m., and 7.15 p. m. on April 10, 11, and 12, respectively, and ending 6 a. m., 6.10 a. m., and 6.15 a. m.

TABLE I.—*Daily growth of date palm before and after midnight, with time of beginning and ending from April 25 to May 20*

Days	Hour growth was resumed	Minutes before sunset	Hour growth ceased	Minutes after sunrise	Growth before midnight	Growth after midnight	Total growth	Excess of growth before midnight	Excess of growth after midnight
	p. m.		*a. m.*		*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Apr. 25 to 26	5.50	--------	6.12	--------	8.0	9.0	17.0	--------	1.0
Apr. 26 to 27	5.57	--------	6.30	--------	10.0	8.5	18.5	1.5	--------
Apr. 27 to 28	5.40	--------	7.30	80	9.5	10.5	20.0	--------	1.0
Apr. 28 to 29	6.50	15	7.05	52	8.0	11.0	19.0	--------	3.0
Apr. 29 to 30	7.12	--------	6.42	29	7.5	9.5	17.0	--------	2.0
Apr. 30 to May 1	5.20	108	6.33	15	8.0	10.5	18.5	--------	1.5
May 1 to 2	7.05	--------	8.10	120	8.0	10.0	18.0	--------	2.0
May 2 to 3	6.15	--------	9.50	189	9.0	13.0	22.0	--------	4.0
May 3 to 4	5.55	85	8.35	223	10.5	12.5	23.0	--------	2.0
May 4 to 5	6.12	69	6.55	50	12.0	12.0	24.0	0.0	0.0
May 5 to 6	7.05	--------	9.00	170	8.5	11.0	19.5	--------	2.5
May 6 to 7	6.25	--------	7.30	80	10.0	10.5	20.5	--------	0.5
May 7 to 8	4.32	161	8.35	145	12.5	10.0	22.5	2.5	--------
May 8 to 9	4.52	148	6.45	33	11.0	8.5	19.5	2.5	--------
May 9 to 10	5.00	148	10.00	220	11.5	9.5	21.0	2.0	--------
May 10 to 11	6.10	70	5.47	21	8.0	6.5	14.5	1.5	--------
May 11 to 12	6.55	32	6.15	--------	9.0	9.5	18.5	--------	0.5
May 12 to 13	7.16	10	6.15	--------	9.5	10.5	20.0	--------	1.0
May 13 to 14	6.50	30	7.50	110	8.5	12.5	21.0	--------	4.0
May 14 to 15	7.00	20	6.12	8	10.0	13.0	23.0	--------	3.0
May 15 to 16	5.22	125	9.00	180	12.0	10.0	22.0	2.0	--------
May 16 to 17	7.10	20	6.45	36	10.0	10.0	20.0	0.0	0.0
May 17 to 18	6.43	51	8.03	60	10.0	10.0	20.0	0.0	0.0
May 18 to 19	6.23	75	8.05	102	9.0	11.0	20.0	--------	1.0
May 19 to 20	6.15	75	7.52	110	12.0	9.5	21.5	2.5	--------
May 20 to 21	6.12	78	8.28	148	10.0	12.0	22.0	--------	2.0

Figure 2 shows the daily growth for nine successive days (May 10 to 19) plotted to a uniform scale; a single line for each night's growth ascending from left to right between the horizontal lines of no growth during sunlight. The vertical lines show the hours of growing time before and after midnight, with the lines of heavy dashes indicating approximately the time of sunset and sunrise.

In a general way both Figures 1 and 2 and Table I show that the growth activity began at a variable time before sunset, progressed rather uniformly through the night and to a period of from a few minutes to two or three hours after sunrise. The excess of growth in the periods before and after midnight appears to depend on the prolongation of the growth period by the light being obscured by clouds and dust, so that normal growth may be regarded as nearly uniform throughout the hours of darkness. It should be noted also that the growth rate in obscured sunlight (for example, the evening of May 15 and the morning of the 16th) is invariably slower than that during full darkness.

Correlated observations on the weather conditions showed that when the air was clearest the beginning of growth was retarded the nearest to sunset, and growth ceased soonest after sunrise. With clouds over the mountain top to the west, obscuring the sunset, or with the air heavy with fine sand driven by winds from the same direction growth began at an earlier hour. After all-night winds which filled the air with dust, or with vapor present in the morning

air, growth was proportionally prolonged after sunrise. In other words, growth in the form of leaf elongation is for the date palm somewhat inverse to the light intensity. It is most active in darkness, nearly or completely checked in bright sunlight, and partial in obstructed light.

GROWTH REACTION TO ARTIFICIAL LIGHT AND DARKNESS

In order to be able to determine more definitely the relation of date leaf growth to light and darkness it was deemed necessary to provide for the exclusion of light at will. In order that otherwise normal growth conditions might not be disturbed, a folding dark cell was constructed which could be placed around a medium-sized palm in the field in a few minutes time. Four panels of light pine framework, each 5 feet wide by 12 feet high, were covered with black enameled cloth (the black surface within) to prevent excessive heating in the sunshine. Three of these panels were hinged together and when erected around the tree the fourth side was slipped into rabbeted

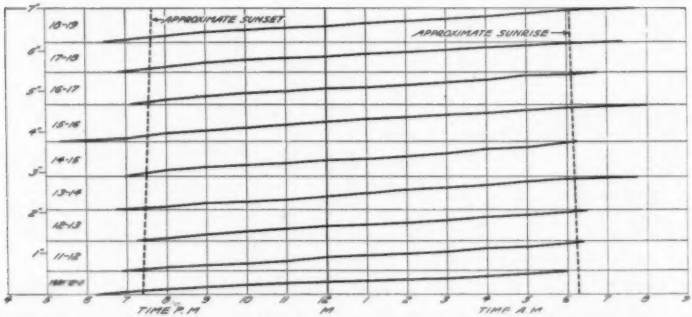


FIG. 2.—Daily and hourly growth of the leaf of Mactoum seedling date palm, plotted from auxanometer sheets, May 10 to 19, 1918

jambs provided to secure light-tight joints and held in place by hinged hasps. With the aid of high stepladders, the top, built like a box lid, was placed in position and also secured with hasps. Thus in a few minutes the date palm, with its spreading leaves drawn by cords into a more erect position (the only disturbance to its natural condition of growth) was inclosed in a completely dark cell or chamber 5 by 5 by 12 feet in size (300 cubic feet capacity). At first the auxanometer and stand were retained inside the dark cell, but it was found more convenient for observation to carry the recording wire through the house wall to the stand with instrument outside.

The first test was made on May 22. After a normal gain during the night of the 21st and 22d, growth had come to a complete standstill at 8 a. m., as shown by the auxanometer tracing, Graph I, Figure 3.

At 10.37 a. m., after 2 hours 37 minutes record of no growth, the dark cell was closed and remained in position till 4.55 p. m. As the actual auxanometer records are somewhat difficult to interpret, they have been transferred to graphs similar to the day and night records in Figure 2, but the time in hours is represented by one-half inch spaces, while the actual leaf growth is represented in the inch and

one-tenth inch vertical spaces. Graph I of Figure 3 shows above the base line the beginning of growth at 7.20 p. m. of May 21, with a rather even gain until 8 a. m. May 22, followed by the horizontal line of no growth to 15 minutes after the dark cell was closed. Active growth was recorded from this time till 5 p. m., five minutes after the dark cell was removed and the tree exposed to full afternoon light, when growth ceased.

From this the horizontal line till 7.25 p. m. indicates that the normal daylight dormant condition as to elongation was resumed in a very few minutes after the plant was exposed to the normal sunlight and continued until the usual night elongation commenced, which was 13 minutes before sunset. In Graph II this night growth is transcribed from 7.25 p. m. May 22 till 8.20 a. m. May 23, from which point a horizontal line of no growth continues till 10.15 a. m., 35 minutes after the dark cell was closed at 9.40 a. m. Apparently when the sunlight was shut out the growth did not start quite so promptly as on the previous day. Here the lack in sensitiveness in the recording mechanism is to be regretted, as a precise reaction time can be only

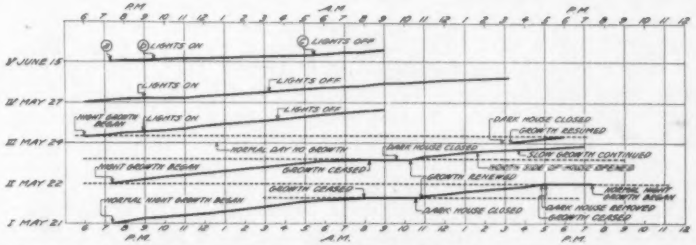


FIG. 3.—Effects of artificial darkness and incandescent light on date-palm growth at the Government Date Garden, Indio, Calif., May, 1918

approximated. On this day the dark cell was opened at 1.37 p. m. by removing the panel on the north side. With the top and three sides remaining in position the tree was still deprived of direct sunlight, receiving only the reflected north light, much of which was absorbed by the black interior walls, giving about the effect of a dull cloudy day. Instead of the growth being wholly checked, as when the dark cell was entirely removed and the tree exposed to full sunlight on the previous day, growth continued as shown by the graph at a less rapid rate than in complete darkness. Therefore exposure to full direct sunlight must be assumed as one of the conditions for growth cessation.

It has been suggested that in securing the resumption of growth within the dark cell at midday other factors than the complete darkness may have been involved, as a marked rise in temperature and an increase in the relative humidity. The reply would be that growth action was recorded before there was time for any very marked change in either temperature or humidity. Moreover the continuation of growth with the north side of the dark sell removed was made under conditions where but little gain in temperature could have resulted, and no increase in humidity, leaving the continuance of growth under partial lighting to be ascribed wholly to the absence of direct sunlight.

GROWTH UNDER ARTIFICIAL LIGHTING

In order to test the converse side of this problem it was next proposed to learn whether active growth in the night could be checked by exposing the tree to artificial lighting. Electric wires from a lighting circuit of 110 volts were carried to the dark cell and two 200-watt incandescent bulbs and two 60-watt bulbs installed, giving an illumination of 520 watts. At 2.53 p. m. May 24, as shown by Graph III, in Figure 3, the dark cell was closed around the tree and active growth was recorded in about 25 minutes. After this growth in darkness had progressed till 9 p. m., the lights were switched on and kept burning till 3.40 a. m., though the dark cell was retained in position till 9 a. m. The gain in growth was practically uniform through the entire period of nearly 18 hours. No checking of growth could be traced to the effect of this degree of illumination. A preliminary trial had, in fact, shown that the cell of 300 cubic feet of space was rather feebly lighted owing to the absorption of light by the black walls. Yet the same number of watts brilliantly illuminated the station office room, 22 by 16 by 10 feet high, or more than 10 times the cubical capacity of the dark cell. The dark cell was next lined with heavy white cotton sheeting and the lighting increased to six 200-watt bulbs, or 1,200 watts. The dark cell was closed at 5 p. m. May 27 and active growth was registered at 6 (Graph III). At 9 p. m. the lights were switched on. This was followed by no growth for two hours or until 11 p. m. At this point the growth was resumed and, until the lights were switched off at 3.15 a. m. May 28, continued at practically the same rate of growth as in full darkness until the dark cell was removed at 3.15 p. m. May 28.

This experiment was repeated in June under the supervision of Bruce Drummond. The lighting was increased to 1,800 watts and the dark cell was erected around the palm on June 15 and normal darkness growth began to be registered shortly after 7 p. m., as shown in Graph V, *a* in Figure 3. At 9 p. m. (*b*) lamps to the volume of 1,800 watts were switched on and continued until 5.30 a. m. of the 16th (*c*). The gain made during these eight hours of illumination was only 3 mm., but from the time the lights were switched off till 9 a. m. of the 16th (3.5 hours) a gain in the dark cell of 3 mm. was also made. In other words, the growth during the eight hours of intense illumination was at the rate of 0.375 mm. per hour, while that during the ensuing 3.5 hours of complete darkness was at the rate of 0.857 per hour. The illumination reduced the growth rate to 43.7 per cent of the rate in darkness. Consequently even so vivid an illumination as that given by 1,800-watt incandescent lamps within this small space of 300 cubic feet, while slowing down the growth rate to less than half, fails to give the complete check which is observed in the ordinary intense sunlight of this station. Evidently a difference in the quality of the rays from the incandescent lamps and those from the sun must be more important than their difference in intensity. The facilities of the Indio field station could take the work no further.

LABORATORY WORK AT WASHINGTON D. C.

A laboratory opportunity for testing the action of date palms under light of a different quality was afforded by the presence in one of the department photographic rooms of two powerful "Cooper-Hewitt"

mercury vapor electric lights working on a 220-volt direct current circuit. These have 50-inch lead glass tubes of "Type P," and are rated by the manufacturers as consuming a current of 385 watts each. Two seedling Thoory palms in 8-inch pots, having leaves in active growth, were selected and prepared for growth measurement by placing in the pot small standards carrying a horizontal gauge piece close to the midrib of the leaf to be recorded. Glass-headed steel ribbon pins were inserted for markers in the leaf rib in contact with the gauge.

A very slight degree of growth could thus be detected by the light being visible between the pin and the gauge, and this space was readily measured by the gentle insertion of one or more thicknesses of paper. Their total thickness was measured with a micrometer caliper gauged to 0.001 inch, but easily read to the half space. As in the artificial light tests at Indio, Calif., it was arranged to record first a period of active growth in complete darkness, then a period of exposure to the light, followed by a second period in darkness.

In preparation for the test the plants were placed in position between the mercury vapor tubes and well below them so that the reflectors would give them the full light. The room was completely darkened from 4.30 to 8 p. m., October 2. Then the 3½-hours' growth in darkness was measured, the pins put down to the gauge and the mercury lights switched on. After an exposure from 8 p. m. until 12 midnight the growth indicated was only the thickness of one sheet of paper (0.002 inch) on palm No. 1, and of two sheets (0.005 inch) on palm No. 2, which may have been a continuation of the darkness growth before the check. Left again in darkness till 8.30 a. m. of October 3, the gauge showed that the growth must have been quickly resumed, as 0.0245 inch of growth was recorded for each plant. The exposure was repeated the night of October 3 under the same conditions, but with a slight modification in time, the results confirming the first night's record. Table II shows the growth in thousandths of an inch for both nights.

TABLE II.—*Growth of two date palms during the nights of October 2 and 3*

Date and hours	Growth made by tree No. 1	Growth made by tree No. 2
	Inch.	*Inch.*
Oct. 2, 4.30 to 8 p. m.	0.0130	[a] 0.0080
Oct. 2, 8 to 12 m.	.0020	[b] .0050
Oct. 2 to 3, 12 m. to 8.30 a. m.	.0245	[a] .0245
Oct. 3, 4 to 8 p. m.	.0250	[a] .0250
Oct. 3, 8 to 11 p. m.	.0025	[b] .0025
Oct. 3 to 4, 11 p. m. to 8.30 a. m.	.0340	[a] .0500

[a] In darkness. [b] Under light.

The interpretation of these records, showing only a minute amount of elongation during the lighted period, seems clearly to be that after the early evening growth in darkness the exposure to the mercury vapor rays checked the growth wholly after a lapse of a few minutes. This reaction period is similar to that found to occur between darkness and sunlight action in the Indio tests.

The rays of the mercury vapor lights appear to have checked the leaf elongation as perfectly as did bright sunlight under Indio conditions, a result not attained with much more intense illumination by incandescent bulbs.

The next step is to compare the spectrum of the incandescent lights and the spectrum of the mercury vapor lights with the solar spectrum. Rays of the solar spectrum, which are lacking in the spectrum of the incandescent lights but present in the spectrum of the mercury vapor lights, must be the important rays in the physiological activity of the date palm, and presumably in that of the other palms which make their leaf elongation chiefly at night.

The subject of the effect of light rays of various colors on the growth of plants has occupied a great deal of attention for more than half a century, and many writers have contributed to its literature. Growing plants in light passed through glass plates of different colors or through colored solutions has shared the field with tests of growth under different portions of the prismatic spectrum. Electric-light culture has also received its full share of attention. The whole subject of the influence of light rays from different regions of the spectrum upon the physiological action of plants is too complex for more than brief consideration.

The writer is not aware, however, of any comparison of growth reaction having been made between light from ordinary incandescent bulbs and light from special illuminants, which either afford a close approximation to pure white light or exclude certain portions of the spectrum, as is done by the Cooper-Hewitt types of lamps.

The Smithsonian Tables 361 and 366 give the following wave lengths, in microns, for the standard colors (*2*):

Violet	0. 44
Blue	0. 46–0. 48
Green	0. 50–0. 52–0. 54
Yellow	0. 56–0. 58
Orange	0. 60–0. 62–0. 64
Red	0. 66–0. 68–0. 70

The same volume, Table 368, gives the visible spectrum as ranging from 0.644 μ to 0.405 μ and the ultra-violet from 0.384 μ to 0.280 μ.

R. D. Mailey, of the engineering department of the Cooper-Hewitt Electric Co., Hoboken, N. J., wrote as follows, in a letter dated October 9, 1918: "The lamps which you are using are made of lead glass, and you will have to keep this in mind, remembering that lead glass does not pass appreciable amounts of light below wave lengths of 3,800 " ($\mu\mu$).

According to the Smithsonian Table 368 (*2*) the ultra-violet rays begin with wave lengths of 0.384 μ, which would leave practically no ultra-violet rays in the radiation from these tubes.

Mr. Mailey did not state the limit of wave length of these tubes in the direction of the red, but fortunately R. A. Steinberge, of the Bureau of Plant Industry, United States Department of Agriculture, had made a spectroscopic analysis of the rays from the identical tubes from which the results under discussion were obtained. These notes he kindly placed at my disposal. Five lines were observed with a hand spectroscope; a bright line in the violet at about 0.405, and one in the blue, a faint line in the blue-green, a strong line in the green, and one in the yellow at about 0.578 μ. Nothing was visible in the higher wave lengths.

W. W. Coblentz, in charge of light investigations in the United States Bureau of Standards, informally places the three light sources under consideration as follows:

Order of intensity

Ultra violet and violet:	Red and infra-red:
I. Sun.	I. Incandescent lamp.
II. Cooper - Hewitt lead - glass mercury lamps.	II. Sun.
III. Incandescent lamps.	III. Cooper-Hewitt lamps.

Summing up, on one side, the factors under which leaf growth occurs, and, on the other, those under which no growth occurs, the following result is obtained:

Date-palm photo-activity

Growth occurs:	No growth occurs:
Normal growth—	*a.* Under bright sunlight.
a. In total darkness, at night or in a closed chamber.	*b.* Under Cooper - Hewitt lead-glass tubes.
b. In chamber with incandescent lights, giving brilliant illumination.	
Partial growth—	
c. During cloudy days.	
d. On clear days; with plant exposed to indirect light.	
e. In closed cell with 1,800-watt illumination.	

Analysis of light conditions

Normal growth:	No growth:
a. In absence of all light rays.	*a.* Under full solar radiation with intense illumination of atmosphere low in water vapor.
b. Under incandescent lamps. Complete spectrum but rays rich in red; no ultra-violet.	*b.* Under Cooper-Hewitt lead-glass tubes; lacking red and orange; containing some yellow, full green, blue, and violet.
Partial growth:	
c. In absence of direct sunlight; proportion of spectrum unknown.	

Jost (*4, p. 127*) concludes:

> A comparison of observations derived from *all* the researches which have been made brings out the following points: (1) Only light of wave lengths between 770 $\mu\mu$ and 390 $\mu\mu$ is conducive to assimilating activity in green plants; these are approximately the same rays which are visible to us; (2) the assimilating effect of different rays is unequal, but still not in such a way that some are active whilst others lying beyond these are quite inactive.

Jost's estimate of available wave lengths, it will be noted, includes considerable infra-red.

For the position of the apex of assimilation, Jost refers to "Figure 27," adapted from Reinke (*9, pl. 1, fig. 6*); but in Reinke's original figure, while the apex is shown at about the Fraunhofer line B, efficient assimilation is shown down to 600 $\mu\mu$, which includes all of the orange, and considerable activity is shown down to the line D, which is about the upper limit of the rays from the Cooper-Hewitt tubes.

Palladin (*8, p. 26*), after discussing many intricate features of the problem, sums the matter up as follows: "Carbon-dioxide is thus seen to be decomposed most rapidly in green plants by the light rays between lines B and C."

In the date-palm experiment leaf growth is continued under brilliant illumination from incandescent lamps rich in red rays, while it is inhibited under Cooper-Hewitt tubes which emit no red rays, but are rich in rays of the shorter wave lengths.

That this is simply a rest period for this particular function, while other vital activities of the tree are in full progress is self-evident.

DAYLIGHT ACTIVITY OF THE DATE PALM

The next inquiry should be, What normal activities of the palm in sunlight are inhibited in darkness? According to general principles of plant physiology they would be: First, photosynthesis or the assimilation of carbon-dioxide; second, the greater proportion of the day's transpiration. From the records of leaf elongation in darkness it appears that in the case of palms such action is diametrically opposed to the daylight activities. The one begins where the other ceases. Whether the leaf elongation during the darkness or absence of direct sunlight is the result of cell multiplication with cell elongation, or of cell elongation only, is a question difficult of determination, but probably the whole cell constructive work of the phillophore is performed during this period.

The intense transpiring activity of date palms during heated days has been referred to in another paper by the writer (*7*) and this is accompanied by photosynthesis on a corresponding scale. There is evidently a close relation between the day's assimilation and the growth of the following night; which is proved by the close correlation between the daily growth curves and temperature curves. But this general relation would not explain the almost immediate growth reaction in response to artificial darkness produced in the middle of a bright day; nor the quick checking of growth when sunlight is restored. If the governing action of the stomates on transpiration is conceded, then by supposing that the stomates close in darkness or partial shade, the checking of transpiration must follow with increased turgescence of the cells in the meristematic region.

In this connection there may be much significance in the recently published studies of Gray and Peirce (*3*) on the reaction of the guard cells and the opening or closing of the stomates of barley, oats, rye, and wheat on exposure to bright sunlight or in its absence. These authors found that under the conditions at Stanford University, Calif., the stomates began to open on bright days soon after sunrise, reaching the fullest expansion from about 11.30 a. m. to 2.30 p. m., and gradually closed as the sun declined. When only portions of the day were bright, the curve of stomatal opening corresponded to these bright portions. On wholly dark days the stomates remained closed. They also found that if two pots of plants in similar condition, both showing the stomates partially open, were taken for experimentation, the plant in the pot subjected to darkness (with other conditions unchanged) soon closed its stomates. But the plant left in continued light (with other conditions unchanged) soon expanded its stomates completely. Reversal of the exposure of these two pots resulted in a reversal of the reactions of the plants.

Now, the conditions as to light and darkness were practically similar to those under which the Indio, Calif., date palms were observed. Where the date palms began growth the cereal plants of Gray and Peirce closed their stomates; where the date palms

fully ceased elongation at sunrise the grain plants showed steadily increased openings of the stomates; and where the date palms resumed growth under darkness supplied at midday, the grain plants closed their stomates.

In the absence of observations on this point it is reasonably safe to assume that the stomates of the palms react toward light in the same manner as those of the grasses.

While the original habitat of the date palm is only a matter of conjecture, in the cultivated state it is at home in the intense light and heat of the desert. Yet the intensity and quality of light under which t thrives, and especially under which it makes its best development of fruit, have heretofore received little attention. But evidence is not lacking that light conditions are second only in importance to temperature conditions for the growth of this tree. Walter T. Swingle (*10, p. 58*) anticipated this in 1904 when he wrote the paragraph on "Sunshine necessary for the date palm."

In the writer's study of the date palm in the northern Provinces of Sudan, a region of intense sunlight and dryness of the air, it was found that the native growers appreciated the necessity of the full exposure of the date-palm crown to the sun's rays. They have a system of allowing several offshoots or "daughters" to grow up to full maturity around the "mother" tree, thus giving a much larger number of stems to the acre than could be tolerated in America. Yet if one of these becomes overshadowed by a stronger growth the fact is at once recognized that its vigor and fruit production are seriously impaired.

SUMMARY

Date palm leaves are formed from the top of the phyllophore or growth center deep in the interior of the terminal bud, protected from light and from wide ranges of temperature.

The leaves, in groups of from three to five, called a palus are pushed forward by basipetal or intercalary increment, no alteration in their length occurring after they reach the light and assume their green color.

Normal growth, as manifested by the pushing up of the leaves from the growth center, is made chiefly in the time between sunset and sunrise, but also at a reduced rate in daylight, when direct sunlight is cut off by clouds. In full sunlight date palm leaf elongation entirely ceases.

Date-palm leaf growth may be induced in darkness obtained by inclosing the plant in a dark chamber, at any hour of the day. Partial growth may be induced in a similar manner by screening the plant from direct sunlight, but giving it exposure to north or reflected light.

Growth begun in darkness was continued at practically the normal rate when the plant was exposed to a battery of Mazda electric lights giving brilliant illumination.

When date plants after beginning growth in a dark room were exposed to the rays of Cooper-Hewitt lead-glass mercury vapor tubes, the inhibiting of growth was as prompt as in direct sunlight.

A spectroscopic analysis of the rays from Cooper-Hewitt lead-glass tubes shows that this light is confined to rays from the shorter wave lengths of the visible spectrum through violet, blue, green, and yellow to about the line D (0.578 μ). The orange and red are completely absent.

It must be concluded, then, that the inhibiting of the date-palm leaf growth in intense sunlight of the desert regions is due chiefly to the action of rays of wave length from about 0.57 μ in the yellow to about 0.405μ in the violet end of the visible spectrum, but invisible ultra-violet rays probably assist in stopping growth.

Photosynthesis is most active in longer wave lengths from the line D at the end of the yellow to lines B and C in the red; thus growth is inhibited by light that has but little potency in photosynthesis and conversely carbon assimilation is favored by light that has but little ability in inhibiting growth.

Growth in absence of direct sunlight is apparently synchronous with the closing of the stomates, checking of transpiration, and increased turgescence in the meristematic tissue.

LITERATURE CITED

(1) Branner, J. C.
1884. The course and growth of the fibro-vascular bundles in palms. Proc. Amer. Phil. Soc. 21: 459–483, illus.

(2) Fowle, F. E.
1923. Smithsonian physical tables. Ed. 7 rev., reprint 2. Smithsn. Misc. Collect., v. 71, no. 1, 458 p.

(3) Gray, J., and Peirce, G. J.
1919. The influence of light upon the action of stomata and its relation to the transpiration of certain grains. Amer. Jour. Bot. 6:131–155, illus.

(4) Jost, L.
1907. Lectures on plant physiology. Translated by R. J. H. Gibson. 564 p., illus. Oxford.

(5) Mason, S. C.
1915. Botanical characters of the leaves of the date palm used in distinguishing cultivated varieties. U. S. Dept. Agr. Bul. 223, 28 p., illus.

(6) ———
1925. The minimum temperature for growth of the date palm and the absence of a resting period. Jour. Agr. Research 31: 401–414, illus.

(7) ———
1925. Partial thermostasy of the growth center of the date palm. Jour. Agr. Research 31: 415–453, illus.

(8) Palladin, V. I.
1923. Plant physiology. Ed. 2 (Amer.) by B. E. Livingston. 360 p., illus. Philadelphia.

(9) Reinke, J.
1884. Untersuchungen über die einwirkung des lichtes auf die sauerstoffausscheidung der pflanzen. Bot. Ztg. 42:1–10, 17–29, 33–46, 49–59, illus.

(10) Swingle, W. T.
1904. The date palm and its utilization in the southwestern states. U. S. Dept. Agr., Bur. Plant Indus. Bul. 53, 155 p., illus.

AN IMPROVED METHOD OF COMPUTATION OF NET-ENERGY VALUES OF FEEDING STUFFS[1]

By MAX KRISS

Institute of Animal Nutrition, Pennsylvania State College

INTRODUCTION

The computation of net-energy values of feeding stuffs from data obtained by means of the respiration calorimeter has been explained in many publications by Armsby and Fries (*1* to *9*).[2] The general principle upon which these computations are based is well known and well understood. Essentially it involves the deductions, from the gross energy of the feed, of the entire expense of utilization of the feed energy for maintenance and production.

While the net-energy conception as promulgated by Armsby remains unaltered, the method of computation of net-energy values followed by Armsby and Fries in their later publications differs in detail from that used by them in the earlier reports, these differences representing improvements resulting from knowledge gained in the course of the experiments.

A further study of this computation in the light of present understanding has led to other improvements as here set forth.

DISCUSSION

The examples given will serve to illustrate the advantage of the latest modification, as compared with the earlier procedures.

Table I, Part A, quoted from Armsby's Nutrition of Farm Animals (*8, p. 272*), is given in that work as an illustration of the method of computing net-energy values for maintenance.

Two periods in which different amounts of timothy hay were fed are compared. The gain of energy is determined for each period by subtracting the heat production from the metabolizable energy. The difference in gain between the two periods, divided by the difference in feed eaten, represents the net energy per unit of feed. More specifically, the net-energy value of the hay is $2{,}028 \div 4.04 = 502$ calories per pound of dry matter.

It will be noticed that the same result may be obtained in this case by subtracting the heat increment per pound of dry matter of hay (433 Calories) from either the metabolizable energy per pound of dry matter of the hay eaten (935 Calories) or from the metabolizable energy per pound of dry matter of the added hay, these two values being identical. This occurrence is explained by the fact that the metabolizable energy per pound of dry matter of the hay is exactly the same in both periods which are compared. This is, however, rarely the case in practical experiments. The numerous sources of

[1] Received for publication Oct. 22, 1924; issued October, 1925.

[2] Reference is made by number (italic) to "Literature cited," p. 484.

error in the determination of the metabolizable energy [3] cause more or less variation in the values per unit of feed in the different periods. Such variations may seriously affect the net-energy values computed by this method. If, for example, one assumes a difference in the metabolizable energy per pound of dry matter of the hay of only 50 Calories between the two periods, without changing the average metabolizable-energy value, the data of Table I, Part A, would be changed into those of Part B, or of Part C.

EXAMPLE 1

TABLE I.—*Computation of net-energy value of timothy hay*

PART A

	Dry matter of hay eaten	Metabolizable energy		Heat produced	Gain of energy
		Per pound dry matter	Total		
	Lbs.	*Cals.*	*Cals.*	*Cals.*	*Cals.*
Period 4	10.21	935	9,544	9,812	−268
Period 3	6.17	935	5,768	8,064	−2,296
Difference	4.04		3,776	1,748	2,028
Difference per pound dry matter of hay			935	433	502

PART B

Period 4	10.21	910	9,291	9,812	−521
Period 3	6.17	900	5,923	8,064	−2,141
Difference	4.04		3,368	1,748	1,620
Difference per pound dry matter of hay			834	433	401

PART C

Period 4	10.21	960	9,802	9,812	−10
Period 3	6.17	910	5,615	8,064	−2,449
Difference	4.04		4,187	1,748	2,439
Difference per pound dry matter of hay			1,036	433	603

In Table I, Part B, the metabolizable energy per pound of dry matter of the hay eaten is 910 Calories in period 4, and 960 Calories in period 3; the average being 935 Calories as in Table I, Part A. The apparent net-energy value of the hay per pound of dry matter is $1,620 \div 4.04 = 401$ Calories, or $834 - 433 = 401$ Calories, instead of 502 calories—a difference of 101 Calories, or 20 per cent. This difference in net-energy value is the direct result of the assumed difference of 50 Calories in the metabolizable energy per pound of dry matter of hay of the two periods compared, although the average metabolizable-energy value of the hay, and heat increment, remained unaltered. The metabolizable energy per pound of dry matter of the added hay is 834 Calories, which is considerably less than the value of the hay eaten in either period 3 or period 4.

[3] For some sources of error in the determination of metabolizable energy see (*11*).

In Table I, Part C, the metabolizable energy per pound of dry matter of the hay eaten is 960 Calories in period 4, and 910 Calories in period 3; the average remaining the same, as in Table I, Parts A and B, namely, 935 Calories. The apparent net-energy value of the hay in this case is 603 Calories per pound of dry matter, as compared with 502 Calories in Table I, Part A, and 401 Calories in Table I, Part B, although the heat increment and the average metabolizable-energy values are the same in all three cases. The metabolizable energy per pound of dry matter of the added hay is in this case 1,036 Calories, which is considerably higher than the value of the hay eaten in either of the two periods.

The availability of the metabolizable energy of the hay, computed from the data which have just been given in Table I, Parts A, B, and C, would be, respectively, $502 \div 935 = 53.7$ per cent; $401 \div 834 = 48.1$ per cent, and $603 \div 1{,}036 = 58.2$ per cent.

It is obvious from the foregoing that the net-energy value computed by this method is affected not only by the difference in metabolizable-energy value of the feed between the two periods compared, but also by the direction of this difference; that is, by whether the determined metabolizable-energy value is greater in the heavier or the lighter of the two rations. Since the net-energy value is computed from the difference in gain between the periods, a relatively small error in the determination of the metabolizable-energy value, which affects the gain directly, may cause a large percentage error in the net-energy value, especially if the difference in gain between the two periods is small. Obviously, errors in heat production would tend to reduce the effect of errors in metabolizable energy, if these errors are in the same direction. If, however, they are in opposite directions, their effect on the gains and on the net-energy value computed by difference would be magnified. It is possible, therefore, to obtain absurd results by this method of computation.

This method was originally used by Armsby and Fries (*1*, *2*, *3*, *4*) in the computation of the availability of the metabolizable energy, which means the net-energy value expressed as percentage of metabolizable energy, and may account to an appreciable extent for the discordant results contained therein.[4]

In their later publications (*5*, *6*, *7*, *9*), Armsby and Fries expressed the net-energy values as per kilogram of dry matter of the feed, and have also recomputed the results of the early experiments on the same basis, using a simplified method of computation. This method consists of averaging the metabolizable-energy values from the several periods, and subtracting from this average the average heat increment of the feed, usually determined by a comparison of the greatest and least amounts of feed eaten. The net-energy value thus obtained is not affected by the factors previously discussed, as in computations by the first method. It is, however, an average value derived in some instances from quite discordant results, and as such does not show the variations in the individual periods.

The new modification described later makes possible the computation of a net-energy value of the feed for each period separately, and besides it has other advantages which will be illustrated in the following examples.

[4] These publications cover experiments 174, 179, 186, 190, 200, and 207, the last three being included in Bulletin 128 of the Bureau of Animal Industry, United States Department of Agriculture.

Since in the following pages the comparison is between only the later method used by Armsby and Fries and the newly modified method of computation, the former will be referred to, for the sake of brevity, simply as the "current method" and the latter as the "new method." It should be borne in mind, however, that what is termed the "new method" of computation is merely a modification of the current method and is based on principles evolved and expounded by Armsby.

EXAMPLE 2, FROM EXPERIMENT 207

In order to make clear the derivation of the net-energy values by the current method and by the new method, a detailed explanation of the several computations involved in both is given in this example (Table II):

TABLE II.—*Data for computation of net-energy values of timothy hay and grain mixture No. 1*

Period No.	Animal	Average live weight	Dry matter eaten		Metabolizable energy		Heat production [a]	Gain of energy
			Timothy hay	Grain mixture No. 1	Per kgm. of dry matter	Total		
		Kgms.	*Kgms.*	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	A	499	2.9349	1.9962	----------	12,061	10,171	+1,890
2	A	519	2.9487	4.7590	----------	20,553	14,035	+6,518
3	A	507	2.9742	----------	2,096	6,235	7,780	−1,545
4	A	514	4.8920	----------	2,076	10,157	9,501	+656

[a] The heat production used in this example, and in those following, has been corrected to a standard day of 12 hours standing and 12 hours lying according to the method of Fries and Kriss (*10*).

THE CURRENT METHOD

COMPUTATION OF THE HEAT-INCREMENT VALUES OF HAY AND OF GRAIN

Using the total observed heat production, corrected to the standard day of 12 hours standing and 12 hours lying as the starting point, the dry matter of the ration (kilograms) and the heat production of one period are compared with the dry matter and the heat production of the other periods. In case the comparison involves one feeding stuff, for instance hay alone, the difference in heat production is div ded by the difference in dry matter. The result is the heat increment per kilogram of dry matter. In case the comparison involves a mixed ration of hay and grain, the difference in heat production due to the added hay is first computed by multiplying the latter by the heat-increment value previously determined from the hay rations. This is subtracted from the total difference in heat production, and the result is divided by the difference in grain to get the heat increment per kilogram of grain. Tables III and IV illustrate this computation, and give the heat-increment values of the timothy hay and of the grain mixture used in the experiment under consideration.

There is only one heat-increment value for the hay, namely, 897 Calories per kilogram of dry matter, which, of course, represents the average heat-increment value of the hay. For the grain there are three values—namely, 1,215 Calories, 1,394 Calories, and 1,319 Calories

per kilogram of dry matter. Of these, the one obtained by comparison of the greatest and least amounts of feed (periods 2 and 3)—namely, 1,319 calories—is considered as the average in the computation of the average net-energy value by the current method.

Attention is called to the fact that the heat-increment values as shown in Tables III and IV are different from those which have been published (*5*). This is the result of the use of revised figures for heat production as previously noted (see footnote to Table II).

TABLE III.—*Computation of heat increment per kilogram of timothy hay*

Period No.	Quantity of dry matter eaten	Heat production
	Kgms.	*Cals.*
Period 4	4.8920	9,501
Period 3	2.9742	7,780
Difference	1.9178	1,721
Difference per kilogram of dry matter		897

TABLE IV.—*Computation of heat increment per kilogram of grain mixture*

Period No.	Quantity of dry matter eaten		Heat production
	Hay	Grain	
	Kgms.	*Kgms.*	*Cals.*
Period 1	2.9349	1.9962	10,171
Period 3	2.9742		7,780
Difference	−.0393	1.9962	2,391
Difference due to hay			−35
Difference due to the grain			2,426
Difference per kilogram of grain			[a] 1,215
Period 2	2.9487	4.7590	14,035
Period 1	2.9349	1.9962	10,171
Difference	.0138	2.7628	3,864
Difference due to hay			12
Difference due to 2.7628 kilograms of grain			3,852
Difference per kilogram of grain			1,394
Period 2	2.9487	4.7590	14,035
Period 3	2.9742		7,780
Difference	−.0255	4.7590	6,255
Difference due to hay			−23
Difference due to the grain			6,278
Difference per kilogram of grain			[b] 1,319

[a] The same value will be obtained by comparing periods 1 and 4.
[b] The same value will be obtained by comparing periods 2 and 4.

COMPUTATION OF THE AVERAGE METABOLIZABLE-ENERGY VALUE OF THE HAY AND OF THE GRAIN

The total metabolizable energy of each hay ration is divided by kilograms of dry matter. The results are metabolizable-energy values per kilogram of dry matter. These values for the timothy hay are (as in Table II) 2,096 Calories and 2,076 Calories for periods 3 and 4, respectively. The average of these—namely, 2,087 Calories—represents the average metabolizable-energy value of the hay used in the experiment.

The metabolizable-energy value of the grain is obtained by a calculation by difference from the hay and grain rations. The metabolizable-energy equivalent of the hay in the mixed ration is first computed by multiplying the average metabolizable-energy value of the hay, previously determined from the hay rations, by the dry matter of the hay of the mixed ration. This is subtracted from the total metabolizable energy of the ration. The remainder is the metabolizable energy of the grain. Dividing this by kilograms of dry matter of the grain gives the metabolizable-energy value of the grain per kilogram of dry matter. These values for the grain mixture are 2,975 Calories and 3,026 Calories per kilogram of dry matter in periods 1 and 2, respectively. The average of these—namely, 3,001 Calories—is the average metabolizable-energy value of the grain.

COMPUTATION OF THE NET-ENERGY VALUES OF THE HAY AND OF THE GRAIN

This computation consists of a simple subtraction of the average heat-increment value from the average metabolizable-energy value previously determined. The result is the average net-energy value of the feed. The average net-energy value of the timothy hay thus computed would therefore be 1,190 (2,087 − 897) Calories per kilogram of dry matter. The average net-energy value of the grain mixture would be 1,682 (3,001 − 1,319) Calories per kilogram of dry matter.

By dividing the average-net energy value per kilogram of dry matter of the feed by its average metabolizable-energy value per kilogram of dry matter, the average percentage utilization of the metabolizable energy may be obtained. According to this computation, the utilization of the metabolizable energy of the timothy hay would be 57.02 per cent (1,190 ÷ 2,087) and of the grain mixture 56.05 per cent (1,681 ÷ 3,001).

THE NEW METHOD

The new method involves the separate determination (1) of the net energy required for maintenance, (2) of the gain of energy by the animal, and (3) of the heat-increment value of the feed.

The heat production of an animal on feed represents a composite of the net energy required for maintenance, in the broad sense; that is, including voluntary muscular activities, and of the energy expenditure, or heat increment, due to the consumption of the feed. By means of the respiration calorimeter, the total heat production is directly measured. The heat-increment value of the feed is determined by a comparison of periods in which different amounts of feed are eaten, as described in the current method, and illustrated in Tables III and IV. This computation assumes that the net energy required for maintenance is the same in the periods which are compared, and that this assumed, although undetermined, maintenance value is canceled in subtracting the heat production of one period from that of another. To illustrate this, if H and H_1 represent, respectively, the heat production of two periods, h and h_1, the heat increment due to the feed, and m the net energy required by the animal for maintenance in either period, then $H = m + h$, and $H_1 = m + h_1$. Subtracting the second expression from the first results in the equation $H - H_1 = h - h_1$.

The new method calls for a determination of the maintenance requirement (m) of net energy. This is obtained by subtracting the computed heat increment, due to the consumption of the feed, from the heat production of each period, in accordance with the principles outlined by Armsby (*8, p. 282*). The average of the several determinations is considered to represent the maintenance requirement of net energy. To this net energy for maintenance is added the gain of energy by the animal in each period, as obtained by subtracting the total heat production from the total metabolizable energy (Table II), and the result represents the total net energy of the ration, from which the net-energy value of the feed is computed. The specific directions for the computations, and the results obtained with the timothy hay and grain mixture No. 1, previously considered, are as follows:

COMPUTATION OF THE HEAT-INCREMENT VALUE OF THE FEED

The computation of the heat increment per kilogram of feed is exactly as in the current method. To avoid repetition, reference is made to the foregoing description of the current method, and to Tables III and IV, which illustrate this computation and give the heat-increment values. If there is more than one value for a feed, the average is used. This is a departure from the current method, in which the value obtained by comparison of only the two extreme rations was used. The reasons for this departure will be given later.

There is only one heat-increment value for the hay—namely, 897 Calories per kilogram of dry matter; and there are three values for the grain mixture—namely, 1,215 Calories, 1,394 Calories, and 1,319 Calories per kilogram of dry matter. The average of these is 1,309 Calories.

COMPUTATION OF THE NET ENERGY REQUIRED FOR MAINTENANCE

Multiply the average heat-increment value per kilogram of the feed by the kilograms of dry matter of each ration. The result is the total heat increment due to the feed. In case of a mixed ration of hay and grain, not fed in the same proportion in the different periods, multiply the kilograms of hay and of grain separately by their respective average heat-increment values, and add the results, to get the total heat increment due to the ration. Subtract the total heat increment from the heat production. The remainder is the net energy required for maintenance. Average the values thus obtained for the maintenance requirement of net energy.

TABLE V.—*Computation of maintenance requirement*

Period No.	Dry matter eaten		Average heat increment per kilogram of dry matter		Total heat increment of ration	Total heat production	Net energy for maintenance
	Timothy hay	Grain mixture	Hay	Grain			
	Kgms.	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	2.9349	1.9962	897	[a] 1,309	5,246	10,171	4,925
2	2.9487	4.7590	897	[a] 1,309	8,875	14,035	5,160
3	2.9742		897		2,668	7,780	5,113
4	4.8920		897		4,338	9,501	
Average							5,066

[a] Average of all values.

COMPUTATION OF THE GAINS OF ENERGY BY THE ANIMAL AND OF THE TOTAL NET ENERGY OF THE RATIONS

Subtract from the metabolizable energy of the ration the total heat production. The remainder is the net energy gained by the animal body. This gain may be negative on low rations. Add to the energy gained by the animal the average net energy required for maintenance. The sum represents the total net energy of the ration.

TABLE VI.—*Computation of the total net energy of the ration*

Period No.	Metabolizable energy	Heat production	Gain	Net energy for maintenance	Total net energy of rations
	Cals.	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	12,061	10,171	+1,890	5,066	6,956
2	20,553	14,035	+6,518	5,066	11,584
3	6,235	7,780	−1,545	5,066	3,521
4	10,157	9,501	+656	5,066	5,722

COMPUTATION OF THE NET ENERGY PER KILOGRAM OF DRY MATTER, AND OF THE PERCENTAGE UTILIZATION OF THE METABOLIZABLE ENERGY OF HAY

Divide the total net energy of the hay ration by the kilograms of dry matter eaten. The result is the net energy value per kilogram of dry matter. To get the percentage utilization of the metabolizable energy, divide the total net energy of the hay ration by the metabolizable energy of the ration and multiply the result by 100.

TABLE VII.—*Computation of the net-energy value of timothy hay*

Period No.	Dry matter of hay eaten	Metabolizable energy of ration	Total net energy of ration	Net energy per kilogram of dry matter	Utilization of the metabolizable energy
	Kgms.	*Cals.*	*Cals.*	*Cals.*	*Per cent*
3	2.9742	6,235	3,521	1,184	56.47
4	4.8920	10,157	5,722	1,170	56.34
Average				1,177	56.40

COMPUTATION OF THE NET ENERGY PER KILOGRAM OF DRY MATTER, AND OF THE PERCENTAGE UTILIZATION OF THE METABOLIZABLE ENERGY OF GRAIN

Multiply the average net energy value of the hay previously determined from the hay rations (Table VII) by the dry matter of the hay in the mixed ration, to get the net energy equivalent of the hay. Subtract this from the total net energy of the ration. The remainder is the net energy of the grain. Divide the net energy of the grain by the kilograms of dry matter of grain eaten to get the net energy per kilogram of dry matter of grain. Multiply the average metabolizable-energy value of the hay by the dry matter of hay in the mixed ration, and subtract the result from the total metabolizable energy of the ration, to get the metabolizable energy of the grain. Divide the net energy of the grain by the metabolizable energy of the grain, and multiply the result by 100 to get the percentage utilization of the metabolizable energy of the grain.

TABLE VIII.—*Computation of net-energy value of grain mixture No. 1*

Period No.	Dry matter eaten		Total metabolizable energy of ration	Metabolizable energy equivalent of the hay	Metabolizable energy of the grain	Total net energy of ration	Net energy equivalent of the hay	Net energy of the grain	Net energy per kilogram dry matter of grain	Utilization of the metabolizable energy of the grain
	Hay	Grain								
	Kgms.	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Per cent*
1	2.9349	1.9962	12,061	6,125	5,936	6,956	3,454	3,502	1,754	59.00
2	2.9487	4.7590	20,553	6,154	14,399	11,584	3,471	8,113	1,705	56.34
Average									1,730	57.67

The net energy values computed by the new method for the timothy hay (Table VII) are 1,184 Calories and 1,170 Calories per kilogram of dry matter, in periods 3 and 4, respectively, the average being 1,177 Calories as compared with 1,190 Calories by the current method. For the grain mixture the net-energy values computed by the new method are 1,754 Calories and 1,705 Calories per kilogram of dry matter in periods 1 and 2, respectively, the average being 1,730 Calories as compared with 1,682 Calories by the current method. There is, likewise, a difference in the average percentage utilization of the metabolizable energy of the hay and grain as computed by the two methods. These differences are due to the differences in procedure. According to the new method, the average of the several determinations of the heat-increment values of the feed is made the basis for the computation of the maintenance requirement of the animal. This departure from the current method is made in consideration of the variations in the heat-increment values obtained by comparison of different periods and of the possible causes for these variations. From the nature of the computation and assumptions involved, any experimental error in the total heat production, or any possible influence of the plane of nutrition, or of difference in activity of the animal, on the net energy used for maintenance, would be reflected solely in the heat-increment value. The influence of such factors on the heat-increment value may be greatly exaggerated, if the difference in heat production and the difference in feed between the two periods compared are small. On this account, the consideration by Armsby and Fries of the value obtained by comparison of the greatest and least amounts of feed consumed as representing an average value in their computations of net-energy values is not without justification. However, since the maintenance requirement of the animal is a factor in the determination of the heat-increment values, the average of several determinations would afford a more accurate basis for the computation of the maintenance requirement during the several periods of an experiment than would a value computed only from the two rations of greatest and least amounts. In the particular example cited above the heat-increment value used for the hay was the same in both methods, there being only one value, while the difference between the average heat-increment value of the grain used in the new method and that used in the current method is only 10 Calories (1,319 and 1,309). This difference alone can not entirely account for the difference in the

average net-energy values of the hay and of the grain as obtained by the two methods. Apparently, the determination of the gains of energy by the animal in each period, and the use of a determined instead of an assumed average value for the net energy required for maintenance, are chiefly responsible for the difference in the average net-energy values as computed by the two methods. As regards differences in live weight in relation to the maintenance requirement of the animal, both methods assume that the variations in weight in one series of experiments are largely due to "fill," that is, to variations in the content of the digestive tract, rather than to any considerable change in the body proper, and that the actual maintenance requirement is not greatly affected.

In order that a full appreciation may be had of the differences between the two methods, in their application to different experiments, the following examples and discussion of results are presented.

EXAMPLE 3, FROM EXPERIMENT 211

TABLE IX.—*Data for computation of net-energy values of mixed hay and hominy chop*

Period No.	Animal	Average live weight	Dry matter eaten		Metabolizable energy		Heat production *	Gain of energy
			Mixed hay	Hominy chops	Per kilogram of dry matter	Total		
	Steer	*Kgms.*	*Kgms.*	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	D	460	6.2042	-------	1,829	11,348	11,710	−362
2	D	432	1.7473	1.7637	-------	9,435	9,665	−230
3	D	470	3.9105	3.9488	-------	21,406	14,123	+7,283
4	D	455	3.4983	-------	1,990	6,958	9,302	−2,344
5	D	428	1.7864	-------	1,834	3,276	8,020	−4,744

* Revised; see footnote to Table II.

TABLE X.—*Heat increment per kilogram of dry matter* *

Feeding stuff	Periods compared	Heat increment per kilogram
		Cals.
Mixed hay	1 and 4	890
Do	4 and 5	750
Do	1 and 5	835
Do	Average of all	825
Mixed hay and hominy chop	2 and 3	1,025
Computed for hominy chop	2 and 5	951
Do	3 and 4	1,134
Do	2 and 3	1,226

* Computed from the revised figures for heat production.

The computation of the average net-energy values of the mixed hay, and of the hominy feed, according to the current method, from the data of Tables IX and X, would be as follows:

MIXED HAY.—Average metabolizable energy per kilogram of dry matter = 1,884 Calories. Heat increment per kilogram of dry matter obtained by comparison of the greatest and least amounts of feed (periods 1 and 5) = 835 Calories. Average net-energy value per kilogram of dry matter, 1,884 − 835 = 1.049 Calories.

HOMINY FEED.—Average metabolizable energy per kilogram of dry matter, computed in a manner explained in example 2 = 3,522 Calories. Heat increment per kilogram of dry matter from periods 2 and 3 (greatest and least amounts of feed), computed in a manner illustrated in Table IV, example 2 = 1,226 Calories (Table X). Average net-energy value, 3,522 − 1.226 = 2.296 Calories.

The computation of the maintenance requirement of the animal, and of the net-energy values of the mixed hay, and of the hominy feed, according to the new method, is as set forth in Tables XI, XII and XIII, respectively.

TABLE XI.—*Computation of maintenance requirement*

Period No.	Dry matter eaten		Average heat increment per kilogram dry matter		Total heat increment of ration	Total heat production	Net energy for maintenance
	Mixed hay	Mixed hay and hominy chop	Mixed hay	Mixed hay and hominy			
	Kgms.	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	6. 2042		[a] 825		5, 118	11, 710	6, 592
2		3. 5110		1, 025	3, 599	9, 665	6, 067
3		7. 8593		1, 025	8, 056	14, 123	
4	3. 4983		[a] 825		2, 886	9, 302	6, 416
5	1. 7864		[a] 825		1, 474	8, 020	6, 546
Average							6, 405

[a] Average of all.

TABLE XII.—*Computation of net-energy values of mixed hay*

Period No.	Dry matter of hay eaten	Net energy for maintenance	Gain	Total net energy of ration	Net energy per kilo. of dry matter
	Kgms.	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	6. 2042	6, 405	−362	6, 043	974
4	3. 4983	6, 405	−2, 348	4, 061	1, 161
5	1. 7864	6, 405	−4, 744	1, 661	930
Average					1, 022

TABLE XIII.—*Computation of net-energy values of hominy feed*

Period No.	Dry matter eaten		Net energy for maintenance	Gain	Total net energy of ration	Net energy equivalent of the hay [a]	Net energy hominy feed	Net energy per kilo. of dry matter of hominy feed
	Mixed hay	Hominy feed						
	Kgms.	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
2	1. 7473	1. 7637	6, 405	−230	6, 175	1, 786	4, 389	2, 489
3	3. 9105	3. 9488	6, 405	+7, 283	13, 688	3, 997	9, 691	2, 454
Average								2, 472

[a] Computed from the average value of table XI.

It will be noted that the computation of the net-energy values of the hominy feed by the new method did not involve, in this case, the computation of a heat-increment value for hominy feed alone. The fact that the hay and the hominy feed were fed in a definite proportion eliminated the necessity of such a computation, inasmuch as the heat increment of the mixed ration of the hay and hominy feed could be made use of directly in determining the value for maintenance in the periods in which the mixed ration was fed (periods 2 and 3, Table XI).

The net energy of the hominy feed computed by this method are 2,489 Calories, and 2,454 Calories per kilogram of dry matter, for periods 2 and 3, respectively, the average being 2,472 Calories, as compared with 2,296 Calories obtained by the current method. The net-energy values per kilogram of dry matter of the mixed hay are 974 Calories, 1,161 Calories, and 930 Calories, per kilogram of dry matter, for periods 1, 4, and 5, respectively, the average being 1,022 Calories instead of 1,049 Calories as by the current method. The considerable deviation of the net-energy value of the hay of period 4 from the values in the other two periods is rather to be expected, since an inspection of the heat-increment values (Table X) indicates that the heat production of period 4 is somewhat low for the ration as compared with the heat production of the other two hay periods, while Table IX shows the metabolizable-energy value in period 4 to be higher than the values in the other two periods, the effect therefore being to make the gains of period 4, and consequently the net-energy value of the hay of this period, relatively high. The individuality of the data is, apparently, preserved by the new computation of the net-energy values.

EXAMPLE 4, FROM EXPERIMENT 212

TABLE XIV.—*Data for computation of net-energy values of alfalfa hay and alfalfa meal*

Period No.	Animal	Average live weight	Dry matter eaten		Metabolizable energy		Heat production [a]	Gain of energy
			Alfalfa hay	Alfalfa meal	Per kilogram of dry matter	Total		
	Steer	*Kgms.*	*Kgms.*	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	H	349	6.6383		2,009	13,337	11,134	+2,203
2	H	349		6.6707	1,984	13,238	10,946	+2,292
3	H	354	5.3202		2,002	10,650	9,843	+807
4	H	349		5.4078	1,971	10,661	9,767	+894
5	H	337	3.0524		2,133	6,510	7,394	−884
6	H	329		3.1549	2,088	6,587	6,868	−281

[a] Revised; see footnote to Table II.

TABLE XV.—*Heat increment per kilogram of dry matter* [a]

Feeding stuff	Periods compared	Heat increment per kilogram	Feeding stuff	Periods compared	Heat increment per kilogram
		Calories			*Calories*
Alfalfa hay	1 and 3	980	Alfalfa meal	2 and 4	934
Do	3 and 5	1,080	do	4 and 6	1,287
Do	1 and 5	1,043	do	2 and 6	1,160
Do	Average of all	1,034	do	Average of all	1,127

[a] Computed from the revised figures for heat production.

This experiment presents a striking example of what the writer believes is the advantage of computing net-energy values according to the new procedure.

According to the current method, the average net-energy value of the alfalfa hay, using the heat increment of the extreme periods (1 and 5, Table XV), would be 2,048 − 1,043 = 1,005 Calories per kilogram of dry matter, and of the alfalfa meal 2,014 − 1,160 (heat increment of 2 and 6) = 854 Calories. By using the average of all heat-increment values of the hay and meal, respectively, the average net-energy value would be 2,048 − 1,034 = 1,014 Calories per kilogram of dry matter of alfalfa hay, and 2,014 − 1,127 = 887 Calories per kilogram of dry matter of the alfalfa meal. Hence, in both cases, the average net-energy value of the meal is considerably lower than that of the hay, when computed by this method.

TABLE XVI.—*Computation of maintenance requirement*

Period No.	Dry matter eaten		Average heat increment per kilogram of dry matter*	Total heat increment of ration	Total heat production	Net energy for maintenance
	Alfalfa hay	Alfalfa meal				
	Kgms.	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1	6.6383		1,034	6,864	11,134	4,270
2		6.6707	1,127	7,518	10,946	3,428
3	5.3202		1,034	5,501	9,843	4,342
4		5.4078	1,127	6,095	9,767	3,672
5	3.0524		1,034	3,156	7,394	4,238
6		3.1549	1,127	3,556	6,868	3,312
Average						3,877

* Average of all values of hay and meal, respectively.

TABLE XVII.—*Computation of net-energy values of alfalfa hay and alfalfa meal*

Feeding stuff	Period No.	Dry matter eaten	Net energy for maintenance	Gain	Total net energy of ration	Net energy per kilogram of dry matter
		Kgms.	*Cals.*	*Cals.*	*Cals.*	*Cals.*
Alfalfa hay	1	6.6383	3,877	+2,200	6,080	916
Do	3	5.3203	3,877	+804	4,684	881
Do	5	3.0524	3,877	−883	2,993	981
Average						926
Alfalfa meal	2	6.6707	3,877	+2,269	6,169	925
Do	4	5.4078	3,877	+891	4,771	882
Do	6	3.1549	3,877	−286	3,596	1,140
Average						982

The net-energy values of the alfalfa hay for the different periods, as computed by the new method, show a fair agreement, the average being 926 Calories per kilogram of dry matter. The net-energy values of the alfalfa meal show a good agreement between periods 2 and 4, and a large deviation from the other values in period 6. Excepting this last period the values for the meal do not differ materially from those of the hay.

Turning to Table XVI, a considerable variation in the values for maintenance in the alternate periods may be noted, these values being lower in the periods in which alfalfa meal was fed. Such a variation can not be accounted for by differences in live weight, as these were very slight (Table XIV). Nor can it possibly be ascribed to the plane of nutrition, for the alfalfa hay rations and the alfalfa meal rations were practically the same. It is also unlikely that the activity of the animal would vary with such a regularity in the alternate periods. Tracing this back to the heat-increment values, in Table XV, it is to be noted that while the heat-increment value of alfalfa meal as obtained by comparison of periods 2 and 4 (934 Calories) is lower than the corresponding value for the hay (980 Calories), the heat-increment values of the meal involving period 6 are considerably higher than the corresponding values for the hay, making the average heat-increment value of the meal higher than that of the hay, and the values for maintenance lower. Whatever the ultimate cause may be, the indication is that when computed by the current method the divergent period 6 is responsible for making the average net-energy value of alfalfa meal considerably lower than that of alfalfa hay, which is hardly possible. It is apparent, therefore, that the new method of computation places the net-energy values on a more accurate plane.

EXAMPLE 5, FROM EXPERIMENT 186

TABLE XVIII.—*Data for computation of net-energy values of red clover hay*

Period No.	Animal	Average live weight	Dry matter eaten	Metabolizable energy		Heat production [a]	Gain of energy
				Per kilogram of dry matter	Total		
	Steer	*Kgms.*	*Kgms.*	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1*a*	I	572	2.9333	2,019	5,922	10,597	−4,675
1*b*			2.9333	2,019	5,922	11,321	−5,398
2*a*			5.0253	2,129	10,690	11,268	−578
2*b*			5.0253	2,129	10,690	11,113	−423
3*a*			4.1391	2,082	8,614	10,605	−1,991
3*b*			4.1391	2,082	8,614	10,677	−2,062

[a] Revised, see footnote to Table II.

TABLE XIX.—*Heat increment per kilogram of dry matter of red clover hay* [a]

Series	Periods compared	Heat increment per kilogram	Series	Periods compared	Heat increment per kilogram
		Cals.			*Cals.*
a	1*a* and 3*a*	7	*b*	1*b* and 3*b*	−534
a	2*a* and 3*a*	748	*b*	2*b* and 3*b*	492
a	1*a* and 2*a*	321	*b*	1*b* and 2*b*	−99

[a] Computed from the revised figures for heat production.

Experiment 186 has been considered by Armsby and Fries as an unsatisfactory experiment, as judged by the abnormally low and divergent heat-increment values. The computation of these values from the revised figures for heat production (Table XIX) reveals this

experiment as even more unsatisfactory. Without going into the causes for these results here, this experiment may serve to show how it is possible, by the new method, using a previously determined maintenance value for the animal, to reveal the general character as to accuracy of the experimental data.

The average net-energy value per kilogram of dry matter of the red clover hay, computed from the data of series *a* according to the current method, would be 2,076 − 321 = 1,755 Calories, and computed from the data of series *b*, impossible values, as indicated in the table.

Experiment 179 was a satisfactory experiment with the same steer, conducted one year before experiment 186, with the same kind of feed as in experiment 186 (red clover hay) in two of the four periods. The maintenance requirement of the animal, computed from the revised figures for heat production, was found to be 6,618 Calories of net energy. The average live weight of the animal during that experiment was 528 kilograms, as compared with 572 kilograms during experiment 186, differing by only 44 kilograms. The maintenance requirement of the steer during experiment 186 may therefore be computed with a fair degree of accuracy in proportion to the two-third power of the live weights as follows:

$$6{,}618 \times \left(\frac{572}{528}\right)^{2/3} = 6{,}981 \text{ Calories.}$$

By the use of this value for maintenance, approximate net-energy values of the red clover hay in experiment 186 may be computed as shown in Table XX.

TABLE XX.—*Computation of net-energy values of red clover hay*

Period No.	Dry matter eaten	Net energy for maintenance	Gain	Total net energy of ration	Net energy per kilogram of dry matter
	Kgms.	*Cals.*	*Cals.*	*Cals.*	*Cals.*
1*a*	2.9333	6,981	−4,675	2,306	786
1*b*	2.9333	6,981	−5,398	1,583	540
2*a*	5.0253	6,981	−578	6,403	1,274
2*b*	5.0253	6,981	−423	6,558	1,305
3*a*	4.1391	6,981	−1,991	4,990	1,206
b	4.1391	6,981	−2,062	4,919	1,188

The net-energy values as computed in Table XX are in fair agreement for periods 2 and 3 of each series, while those of period 1 are abnormally low. This points to an abnormally high heat production in period 1 of each series, as the variation in the metabolizable-energy values in the different periods is only slight (Table XVIII). In other words, the results given in Table XX indicate that period 1 of each series was mainly responsible for rendering the whole experiment worthless when computed by the current method. The new computation indicates that the results of periods 2 and 3 of both series *a* and *b* are fairly accurate. The advantage of such a computation is obvious.

SUMMARY

By a critical analysis of the methods of this institute for the computation of the net-energy values of feeds, from results of respiration calorimeter experiments, previously unsuspected defects have been revealed.

These defects have seriously affected the general character, as to accuracy, of the existing evidence in the field of net-energy determinations.

Two procedures have been used in computing net-energy values, and have been widely quoted. Both are correct in principle, but tend to magnify experimental errors.

In the earlier method the net-energy value of a feed was determined by comparison of the gains in energy yielded by rations of different amounts. The feed represented in the computation was only the difference between the two rations, the relatively extensive maintenance requirement of net energy not being directly involved, the effect, therefore, being to relate the entire error of the determination to the small amount of feed represented by the gain.

The later method is an improvement over the earlier one in that the above-mentioned exaggeration of errors is eliminated. It tends, however, to obscure the individuality of the data, and to exaggerate the effects of assumptions necessarily involved.

A revised method of computation of net-energy values is presented which tends to eliminate the exaggeration of errors and to preserve the individuality of the data, and makes possible the computation of a net-energy value of a feed for each of a series of periods, instead of giving only one average value representing results of two or more periods, as accomplished by the earlier methods. It thus also provides an improved basis for judgment as to the consistent character of an experiment as a whole.

LITERATURE CITED

(1) Armsby, H. P., and Fries, J. A.
1903. The available energy of timothy hay. U. S. Dept. Agr., Bur. Anim. Indus. Bul. 51, 77 p., illus.

(2) ——— and Fries, J. A.
1905. Energy values of red clover hay and maize meal. U. S. Dept. Agr., Bur. Anim. Indus. Bul. 74, 64 p., illus.

(3) ——— and Fries, J. A.
1908. The available energy of red clover hay. U. S. Dept. Agr., Bur. Anim. Indus. Bul. 101, 61 p., illus.

(4) ——— and Fries, J. A.
1911. The influence of type and of age upon the utilization of feed by cattle. U. S. Dept. Agr., Bur. Anim. Indus. Bul. 128, 245 p., illus.

(5) ——— and Fries, J. A.
1915. Net energy values of feeding stuffs for cattle. Jour. Agr. Research 3: 435–491, illus.

(6) ——— Fries, J. A., and Braman, W. W.
1916. Energy values of red-clover hay and maize meal. Jour. Agr. Research 7: 379–387.

(7) ——— and Fries, J. A.
1917. Energy values of hominy feed and maize meal for cattle. Jour. Agr. Research 10: 599–613.

(8) ———
1917. The nutrition of farm animals. 743 p., illus. New York.

(9) ——— and Fries, J. A.
1918. Net energy values of alfalfa hay and of starch. Jour. Agr. Research 15: 269–286.

(10) Fries, J. A., and Kriss, M.
1924. Metabolism of cattle during standing and lying. Amer. Jour. Physiol. 71: 60–83.

(11) Kriss, M.
1925. A comparison of direct and indirect calorimetry in investigations with cattle. Jour. Agr. Research 30: 393–406.

IDENTITY OF THE MEALYBUG DESCRIBED AS DACTYLOPIUS CALCEOLARIAE MASKELL[1]

By HAROLD MORRISON

Entomologist, Fruit Insect Investigations, Bureau of Entomology, United States Department of Agriculture

INTRODUCTION

The increasing importance of the elongate gray mealybug found in many parts of the world on sugar cane, both as a pest and as a subject for study as a possible carrier of the sugar-cane mosaic disease, has made it highly desirable to verify or correct the scientific name by which the species is recognized in technical literature. The specific name *calceolariae*, first applied to a mealybug more than 50 years ago, has in recent years been used very frequently in published references to this sugar-cane mealybug, although it has been recognized for some time that there was a legitimate question as to the correctness of the application.

In the course of preliminary studies on the large Maskell collection of scale insects, very generously loaned to the United States Bureau of Entomology by the New Zealand Department of Agriculture, a certain amount of material bearing on this subject was obtained, but nothing from which definite conclusions could be established. A recent appeal for additional specimens, made to J. G. Meyers, of the Biological Laboratory of the New Zealand Department of Agriculture, and transmitted by him to Gilbert Archey, of the Canterbury Museum, Christchurch, New Zealand, has resulted in the receipt from the latter of a few more specimens, some of which are mounted and accompanied by data indicating without question that they were before Maskell at the time he prepared his original description.

From the material thus accumulated it has been possible, after extended and careful study, to work out the identity of the species represented, if not completely, at least to an extent sufficient to meet the practical needs of the situation. This discussion attempts to restrict properly the use of the name *calceolariae*, and to segregate and correctly designate the different species which have been known by this name.[2]

HISTORY OF MASKELL'S USE OF NAME

The species was first described by Maskell in 1879 (*9, p. 218–219*),[3] who then stated that "this insect is effecting great destruction in the public gardens in Christchurch amongst the Calceolarias and upon several native plants such as Traversia, Cassina, etc." In the original description the color is given as pink covered with white meal, and the shape is indicated as oval in the accompanying figure. The body is said to be very oily.

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[1] Received for publication October 25, 1924; issued October, 1925.

[2] The drawings illustrating the structural characteristics of the species described here have been prepared under the writer's direction, those for *boninsis* by Emily Morrison, and the others by Leola J. Kruger.

[3] Reference is made by number (italic) to "Literature cited," p. 499.

Maskell's second reference to the species was in 1884 (*10, p. 138–139*), when the insect was reported from Stewart Island, southern New Zealand, on Phormium and on a grass (Danthonia). The length of the Danthonia specimens, more than ¼ inch, was noted. and the species was considered to be indigenous.

The third reference was made in 1887 (*11, p. 100*), when the species was described again and reported as occurring on Calceolaria and *Phormium tenax* at Christchurch, and on Danthonia from Stewart Island. A colored figure of the species as it occurs on Phormium was given.

The species was next mentioned in 1890 (*12, p. 149–150*), when Maskell stated that examples received on sugar cane from Fiji were, to him, indistinguishable from *calceolariae*.

Another reference to the species was made in 1894 (*13, p. 89*), when specimens from Napier (New Zealand) on *Cordyline australis* were discussed. The same note suggested that a mealybug from northern Mexico is this species, since a drawing of the foot of this last exactly corresponds to that of *calceolariae* and since he (Maskell) has recorded this species from sugar cane.

In a "Synoptical list of the Coccidae reported from Australasia and the Pacific Islands up to December, 1894" (*14, p. 24–25*), Maskell recorded this species from New Zealand on *Calceolaria* sp., *Cordyline australis*, *Danthonia cunninghamii*, and *Phormium tenax*, and from Fiji on *Saccharum officinarum*.

Maskell's final reference to the species came in 1897 (*15, p. 322*) when he described as new a variety, *minor*, from Mauritius on roots of "onion grass."

MASKELL MATERIAL AVAILABLE FOR EXAMINATION

The following is a list of Maskell specimens, identified as this species, which have been available for examination:

(1) Original or type slides, "from Traversia, old female, June 1878"; "from Traversia, old females, June 1878"; "from Traversia, 2 young insects, June 1878"; "from Calceolaria, Female, 2nd stage, June 1878."

(2) Some slide mounts from specimens in formalin, received with the preceding slides from the Canterbury Museum, Christchurch, New Zealand, and labeled simply "*Dactylopius calceolariae*."

(3) Four slides from the Maskell collection, one each "From Danthonia (grass); (Stewart's Island), Adult female, Sept. 1880"; "adult females, 1886"; "larva, 1893"; "var. *minor*, adult female, 1896."

(4) Some slides of various stages prepared from the unmounted Maskell collection material.

(5) Two slides of different stages of var. *minor* prepared from the unmounted Maskell collection material.

STATUS OF THE MATERIAL LISTED

(1) It is obvious that only the first four slides listed can be positively considered as having been examined by Maskell at the time he described the species, and these, therefore, include the type.

(2) Of the four original slides, one, that from Calceolaria, bears only a poorly preserved second-stage female. This species is un-

doubtedly a close relative of *Pseudococcus citri* (Risso), differing from specimens of the same stage of that species, so far as the writer can determine, only in the possession of relatively large, short tubular ducts scattered adjacent to the cerarii, at least in the abdominal region. Since it is not possible to identify this definitely, it has been excluded from further consideration as part of the type material of the species.

(3) The three Maskell slides from Traversia therefore become the types of *Dactylopius calceolariae* of Maskell and the redescription given below under the name *Pseudococcus calceolariae* (Maskell) has been drawn up from the three adult females, all imperfect, present on these slides.

(4) The species mentioned by Maskell in 1883 as having been found on Danthonia at Stewart Island is distinct from both of the species already mentioned, and since it has not been recognized as identical with any of the described species in the group, it has been described here as new under the name *Trionymus danthoniae*.

(5) No specimens definitely known to have formed a part of the material on which the 1883 record on Phormium was based are available, so the actual status of this record is not determinable. However, in view of the widespread occurrence on Phormium of the species discussed in the next paragraph, it seems a reasonable assumption that the portion of Maskell's 1883 record referring to "*calceolariae* on *Phormium*" actually refers to the following species.

(6) Maskell's 1887 record on *Phormium tenax* from Christchurch is considered to be plainly represented by the single slide bearing two adult females, dated 1886. The specimens on this slide are specifically identical with some, without data other than name, mounted from the Maskell general collection, and with specimens on *Phormium tenax* from Berkeley, Calif., and despite certain apparent descrepancies, agree well with the description of *Pseudococcus diminutus* published by Leonardi. All the published records of *P. calceolariae* Mask. from the host *Phormium tenax* can therefore, in all probability, be referred to Leonardi's species *diminutus*.

(7) The specimens on sugar cane from Fiji, the record of which was published by Maskell in 1890, are not definitely represented by any of the specimens available for examination, and it is therefore impossible to establish with certainty the identity of the species to which this reference applies. In view of the wide distribution of the elongate gray mealybug of sugar cane, which has almost always been designated by the name *calceolariae* by other writers, it is a reasonable, although at present unverifiable, assumption that Maskell's specimens on sugar cane from Fiji were this species, that is, the *calceolariae* on sugar cane of authors. To this species the writer, in making identifications, has applied the name *boninsis* Kuwana, since the description given by Kuwana, so far as it extends, entirely coincides with specimens of this elongate gray sugar-cane mealybug already reported from so many parts of the world that its eventual discovery may be expected practically everywhere that sugar cane is grown extensively.

(8) The Maskell slide of a larva dated 1893 evidently is the species reported from Napier on *Cordyline australis*. None of the other specimens available can be definitely associated with this record, and the identity of the species can not be determined with

certainty from the larva. However, since the host is included in the same plant family as Phormium, since the general locality of the collection is identical with that of the species from Phormium, and since the larval characters, so far as they can be observed, do not contradict the conclusion, it is reasonable to assume that the species mentioned in this record is identical with that occurring on Phormium, and it is tentatively given such an association.

(9) After an examination of the type specimens, Maskell's *Pseudococcus calceolariae*, variety *minor*, has been placed as a synonym of *Pseudococcus citri* (Risso).

(10) Certain specimens, obtained from the unmounted portions of the Maskell and Canterbury Museum collections of "*calceolariae*," are not identical with any of the species already discussed and can not be positively associated with any of the Maskell records not represented by properly identified specimens. One of these species is characterized here, despite its lack of definite host or distribution records, in the hope that such description will expedite the discovery of its habitat and host relationships. The condition of the specimens of the other species is such as to preclude the possibility of accurate description, although it can probably be recognized by direct comparison if ever rediscovered.

DESCRIPTION OF SPECIES

Genus PSEUDOCOCCUS Westwood

Pseudococcus ambiguus, new species (fig. 1)

ADULT FEMALE.—(Described from a single mounted specimen.) Length 4 mm., width 2 mm., uniformly elongate oval; antennae broken, legs broken except coxae, the hind pair with a few large pores; beak small, elongate conical, length 153 μ, width 107 μ, somewhat obscurely 2-segmented; with the cephalic pair of cerarii present, each composed of 3 spines surrounded by a cluster of triangular pores without definitely associated setae; in addition with 4 more or less distinctly recognizable cerarii on each half of the posterior abdominal segments, the apical and preapical each with a densely crowded cluster of triangular pores, the remainder with scattered clusters, apical cerarii each with 4 long spines and 5 accessory setae, preapical with 6 to 8 spines of unequal size and 2 to 3 accessory setae, next two with 3 small spines and a few pores but no accessory setae, last (anterior) with 2 slender spines and a few pores only; remaining cerarii not definitely developed, but their location sometimes hinted at by presence of 1 or 2 well separated, slender spines accompanied by a slightly closer grouping of the adjacent triangular pores; anal lobes only slightly produced, no ventral chitinized thickening evident, apical setae broken, but, from diameter of base, apparently somewhat longer than anal ring setae; anal ring not unusual, with the usual inner and outer pore bands and 6 setae, the longest of these about 180 μ, pores of the usual types, the triangular widely scattered over both the dorsal and the ventral surfaces, the multilocular disk pores apparently limited to two small clusters, one anterior, the other posterior to the genital opening, plus a few in the middle of the segments just anterior to these; small tubular ducts present but rare, apparently confined to the posterior ventral abdominal area; body setae rather small and not conspicuous, the ventral averaging distinctly longer than the dorsal, more slender and varying considerably in size; ventral cicatrix moderately large, transverse, irregular in shape.

PREADULT FEMALE.—(Based on a single mounted specimen.) In general resembling the adult, but with somewhat smaller size or fewer numbers of various structures, and with multilocular disk pores wanting.

The holotype of this species was mounted from a pinned specimen included among the specimens of *Pseudococcus calceolariae* in the Maskell collection. As has already been demonstrated in this paper, the species is not *calceolariae*, and it is likewise possible to

reach the definite conclusion that it is not *Pseudococcus glaucus*, as originally described by Maskell, from the Maskell material of which the preadult female was obtained. The writer has not been successful in associating these specimens with any of the species described by Maskell or others, and although reluctant to describe it from the limited material available for study, he believes that it can be readily recognized from the description whenever it may be found in the future, owing to the apparently unusual and distinctive cerarian characters, and that its association with the species complex discussed in this paper makes its characterization practically necessary.

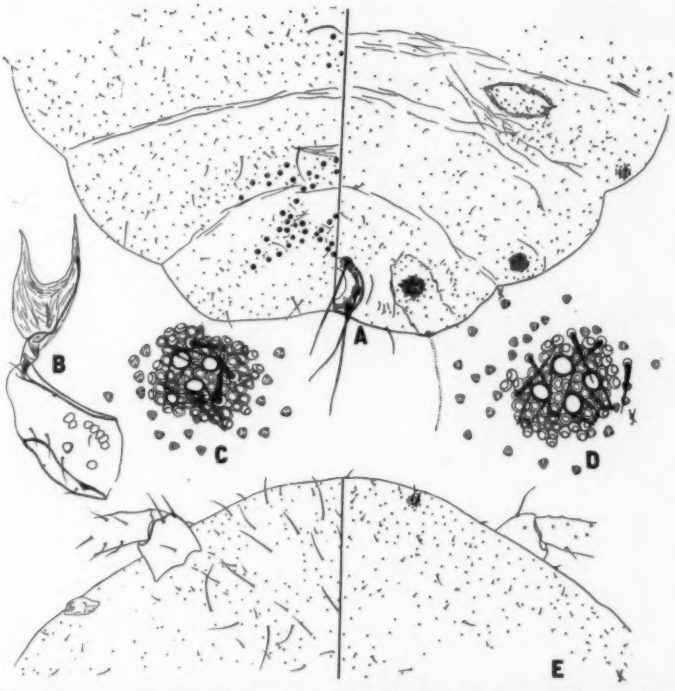

FIG. 1.—*Pseudococcus ambiguus*, adult female: A, apex of abdomen, ×96; B, posterior coxa, ×96; C, preapical cerarius, ×424; D, apical cerarius, ×424; E, apex of head, ×96

Although no definite distribution or host data are available, it is assumably a New Zealand species.

The types are in the United States National collection of Coccidae.

PSEUDOCOCCUS BONINSIS KUWANA (figs. 2, 3)

ADULT FEMALE.—External appearance well described by Fullaway (*3*), and others, and not treated here; size of body, as mounted, varying considerably; well-developed individuals about 4.5 mm. long by 2.5 mm. wide; derm entirely membranous; antennae normally 8-segmented, the average lengths of the segments of several individuals in microns as follows: I, 67; II, 68; III, 43; IV, 31.5; V, 41; VI, 34; VII, 41; VIII, 98; legs not unusual, hind coxae with a varying number of tiny and often rather indistinct pores on basal portion, hind femora with some

large, faint areolations, not always evident; tibia about twice length of tarsus, about two and one-half times in hind pair, claw without denticle, both pairs of digitules long, slender, knobbed, but those of claw stouter; beak elongate conical, fairly evidently 2-segmented; series of cerarii incomplete, one pair on head and the 5 or 6 posterior abdominal pairs only present, each of those on head composed of 2 spines, a few triangular pores and 1 or 2 accessory setae, rarely with one or both of the spines elongated and setalike, still more rarely with 3 spines, the apical abdominal pair each large, with 2 spines, a loose cluster of pores and several accessory setae, not underlaid by any definite chitinous thickening, the remaining pairs with the spines progressively smaller anteriorly, each with 2 spines, a few triangular pores and one or more accessory setae, spines in each of sixth or anterior developed abdominal cerarii most often elongate, setalike; anal lobes hardly protruding, apical seta fairly large, about 100 μ long when uninjured, longest anal ring seta about 64 μ; with the usual types of pores and ducts, triangular disk pores well distributed over body both dorsally and ventrally, apparently scattered or in very poorly defined broad segmental bands, multilocular disk pores confined to the ventral abdominal region, in a large cluster

FIG. 2.—*Pseudococcus boninsis* adult female. Apex of abdomen, × 185

around the genital opening, and in two transverse rows or narrow bands on the two ventral segments anterior to the genital clusters, in no case, so far as has been determined, occurring in the head, thoracic, or anterior abdominal region, and none of the bands or clusters attaining the body margin at any point; only medium or rather small, short tubular ducts present, these, in the abdominal area, most abundant along the body margin adjacent to the cerarii, but present to some extent in the median area both dorsally and ventrally; body setae, both dorsally and ventrally, comparatively long and slender, showing considerable variation in length, those of ventral area actually and relatively longer; anal ring not unusual, with inner and outer single pore bands and 6 setae; ventral cicatrix of medium size, roughly quadrate, with rounded corners.

PREADULT FEMALE.—In general, rather closely resembling the adult except for smaller size and extent of development of the different structures; multilocular disk pores wanting.

This species has been redescribed from a considerable series of specimens, all from sugar cane, from Argentina, Bermuda, Brazil,

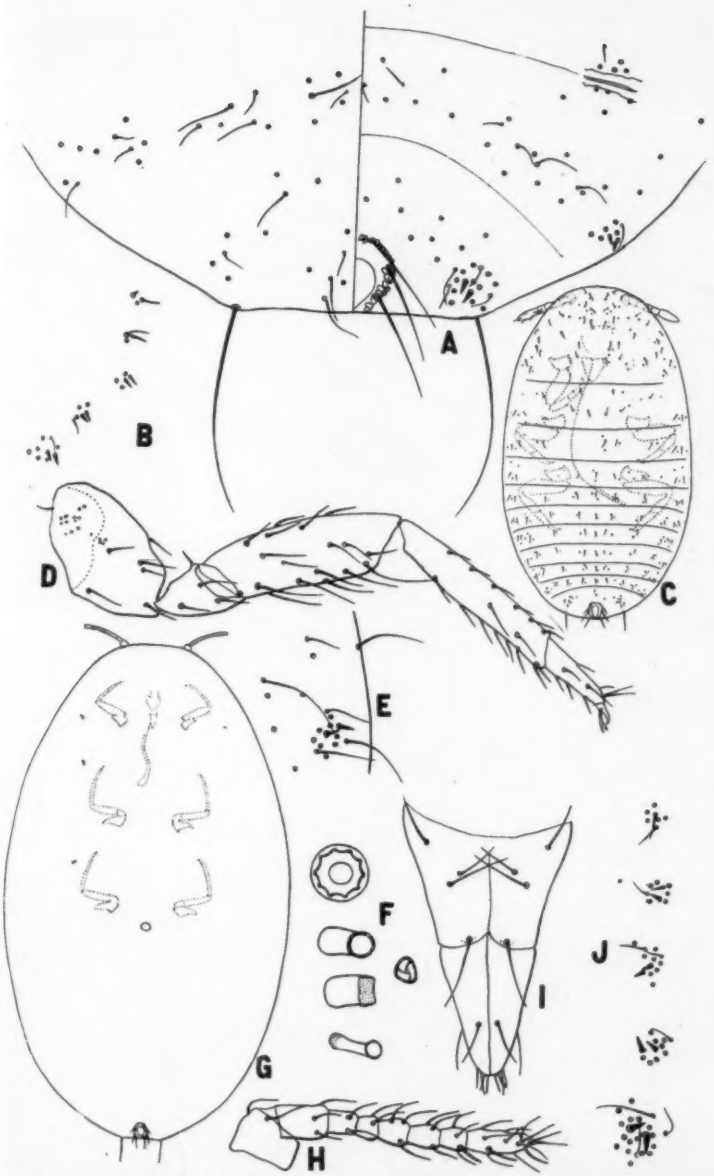

FIG. 3.—*Pseudococcus boninsis:* A, preadult female, apex of abdomen, × 230; B, same, series of abdominal cerarii, × 230; C, larva, outline, optical section, × 60; D, adult female, posterior leg, × 115; E, same, cerarius on head, × 230; F, same, types of pores on body, × 1275; G, same, outline of body, optical section, × 17.5; H, same, antenna, × 115; I, same, beak, × 230; J, same, series of abdominal cerarii, ×230

Canal Zone, District of Columbia (greenhouse), Dominican Republic, Florida, Georgia, Hawaiian Islands, Japan, Louisiana, and Panama. It has, unfortunately, not been possible to obtain specimens from the type material to prove absolutely the correctness of the association of these specimens with the species described by Kuwana on sugar cane from the Bonin Islands.

The only exceptions to the use of the name "*calceolariae*" for the gray sugar-cane mealybug in recent literature appear to be those found in the references of Kotinsky (*6*) and Ehrhorn (*1; 2, p. 237*). The first writer evidently confused and reversed the application of specific names to the two species *boninsis* and *sacchari* (Cockerell). The second author, on the basis of a comparison of specimens by E. E. Green, assigns the species *calceolariae* on sugar cane of authors to the species *saccharifolii* of Green. If one is to accept Green's original description as accurate, there is no possibility that the form here designated as *boninsis* can be identical with *saccharifolii*, since Green (*5, p. 23–24*) states very definitely that there is a group of about 8 stout pointed spines on each lobe of the apical abdominal segment and that the other segments, including both abdominal and thoracic, bear from 4 to 6 similar spines on processes on each margin. This description of the cerarian spines and that given of the distribution of the multilocular disk pores is so precise and so very different from the condition in *boninsis* (*calceolariae* on sugar cane of authors) that there would seem to be no possibility whatever of confusing the two species. Should the description prove to be seriously erroneous, and the type specimens actually identical with the species here designated as *boninsis*, Green's name will, from the dates of publication of the species, take precedence, since *boninsis* was described by Kuwana (*7, p. 161–162*) in 1909, more than one year later than the publication date of Green's species.

The latest contribution to this subject is that made from Hawaii by Fullaway (*3, p. 312–314*), where the name *Trionymus calceolariae* is used for the species under discussion. None of the specimens examined shows clearly the heavy ventral, chitinized anal lobe thickening emphasized by Fullaway in his drawing, although in many specimens the structure is vaguely suggested.

PSEUDOCOCCUS CALCEOLARIAE MASKELL (fig. 4)

ADULT FEMALE.—(Described from slide mounts only. Nothing available regarding external appearance, color, or secretion. See Maskell description for this.) Length as mounted averaging about 3 mm., width a little more than 1.5 mm., derm clearing completely except for appendages, and a tendency towards a thickening underlying each anal cerarius; antennae normally 8-segmented; measurements in microns about as follows: I, about 64; II, 40 to 78, average about 65; III, 57 to 93, average about 72; IV, 33 to 57, average about 46; V, 36 to 64, average about 48; VI, 36 to 43, average about 40; VII, 43 to 50, average about 47; VIII, 93 to 117, average about 107; legs not unusual, hind pair, so far as can be determined, without pores, except possibly a few large faint ones, femur slightly longer than tibia, claw stout, somewhat curved, without denticle, claw digitules rather stout, swollen at apices, exceeding claw, tarsal digitule slender, only slightly knobbed, likewise very slightly exceeding claw; beak elongate conical, appearing distinctly 2-segmented; with 17 pairs of cerarii made up of spines, triangular pores, and accessory setae, all, except the two or three anterior pairs, with 2 spines in each, these with 3, the spines of the posterior cerarii much larger than the others, intermediate cerarii with, on the average, about 10 pores and 2 accessory setae, but these numbers varying, each posterior cerarius with as many as 10 large accessory setae and around 50 triangular pores, these scattered, each posterior cerarius underlaid by a chitinous thickening, fairly distinct in stained mounts; apical seta about 200 μ long, without any definite ventral thickening accompanying it; anal ring typical for the genus.

with inner and outer pore bands and 6 setae averaging about 196 μ long; body with the usual type of pores, the small triangular sort occurring both dorsally and ventrally in loose and indistinct transverse bands in the abdominal region, apparently indiscriminately scattered anteriorly, multilocular disk pores present ventrally in 5 transverse segmental rows in the abdominal region; large tubular ducts apparently confined to 1 opposite or nearly opposite and dorsad of each cerarius, and 1 or perhaps sometimes more on the median line anterior to the anal ring, small tubular ducts present in a loose cluster beneath each of the posterior 5 or 6 pairs of abdominal cerarii, the size of the clusters diminishing anteriorly, number and arrangement of these pores apparently showing con-

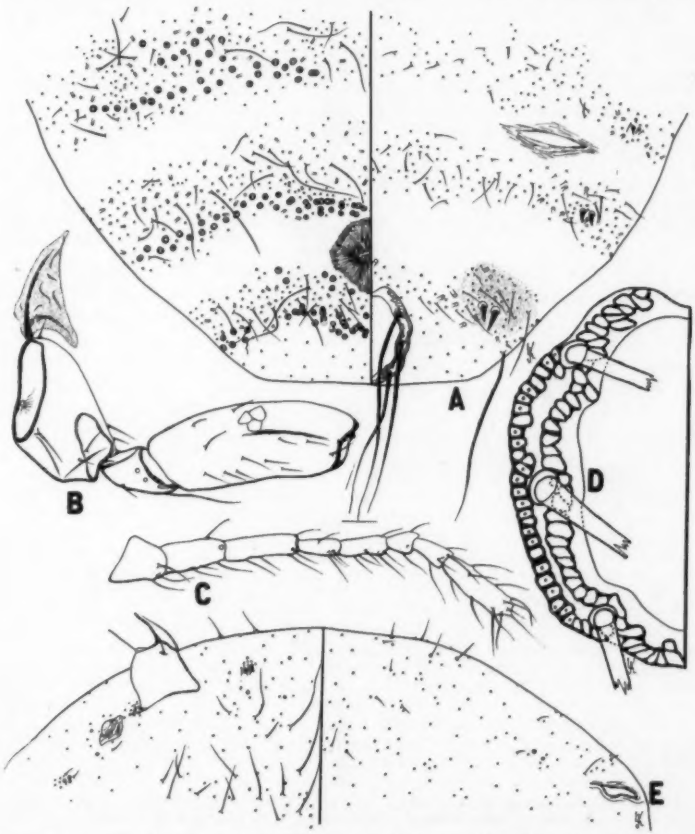

FIG. 4.—*Pseudococcus calceolariae*, adult female: A, apex of abdomen, × 120; B, portion of leg, × 120; C antenna, × 120; D, anal ring, × 530; E, apex of head, × 120

siderable variation, and in indefinite transverse ventral rows accompanying the large disk pores; dorsal setae small, in scattered transverse bands, ventral setae varying, but mostly much longer and relatively more slender, quite conspicuous, particularly anterior to the mouth parts; with a single, unusually large, quadrate ventral cicatrix.

This species has been redescribed from the three imperfect adult females from the original Maskell slide mounts having the following data: "from *Traversia*, June 1878."

This insect should be added to the group of species including *maritimus* (Ehrhorn), *adonidum* (Linnaeus) and *comstocki* (Kuwana). It resembles the last more closely than any other mealybug that the writer is familiar with, having the general organization of the pores and ducts and the posterior cerarii almost identical, but differing in apparently lacking a ventral chitinized thickening, and, on the head, in having the dorsal body setae shorter and more conspicuously

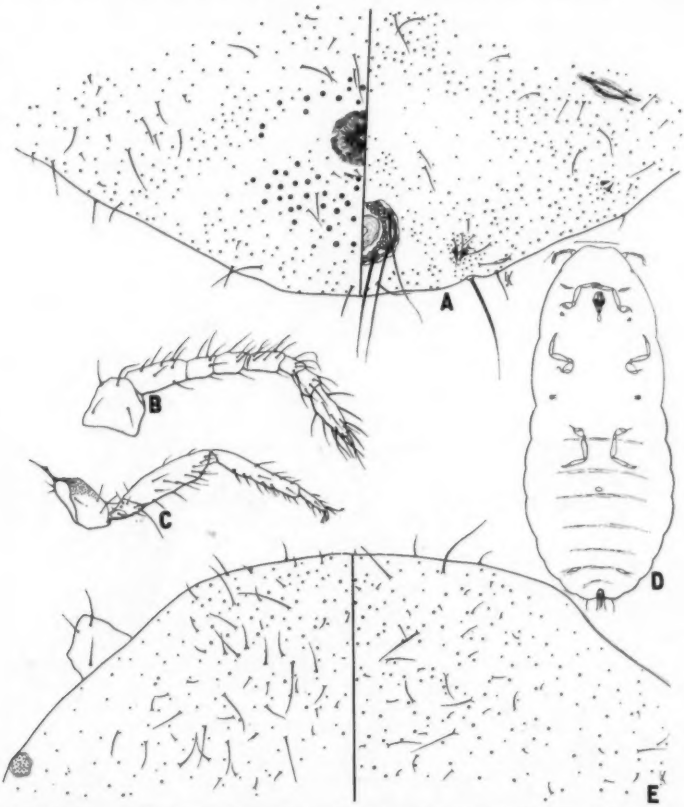

FIG. 5.—*Trionymus danthoniae*, adult female: A, apex of abdomen, × 96; B, antenna, × 96; C, posterior leg, × 96; D, outline of body, optical section, × 10; E, apex of head, × 96

contrasted with the ventral in size, and finally in having fewer multilocular disk pores and ventral tubular ducts than are present in *comstocki*.

Genus TRIONYMUS Berg

Trionymus danthoniae, new species (fig. 5)

ADULT FEMALE.—(See Maskell paper (*10, p. 138–139*) for all available information regarding external appearance; described here from slide mount only.) Length 5.75 mm., width 2.5 mm., nearly parallel-sided with ends of body rounded, segmental constrictions more or less evident; antennae normally 8-segmented, average length of the segments in microns about as follows: I, 80; II, 89; III, 52;

IV, 45; V, 57; VI, 34; VII, 43; VIII, 86; the second segment thus the longest; legs not unusual, hind coxae with pores near base, at least, claw rather stout, somewhat curved, claw digitules stouter than those of tarsus, both pairs exceeding the tip of the claw, tibia and femur about equal in length, tibia about three times length of tarsus; beak stout conical, about as broad at base as length; with only the two posterior pairs of cerarii with the spines developed, these with 2 stout conical spines accompanied by several triangular pores in each, and with a loose cluster of 4 to 5 setae outside the spines; location of some additional cerarii indicated by presence of 1 or 2 larger setae at appropriate place on body margin, but no other definite cerarii present; anal lobes, as such, not indicated, apical seta large, about 196 μ long, without ventral chitinous thickening but with a ventral subapical seta about 90 μ long; body with small triangular disk pores of the normal type, occurring both dorsally and ventrally in indistinct transverse bands of widely scattered pores, with circular multilocular disk pores in indefinite transverse bands of scattered pores in the posterior abdominal region, with a few pores distributed apparently indiscriminately over the midventral area as far anteriorly as around the base of the mouth parts, and with numerous short tubular ducts distributed much in the same fashion as the triangular pores, but most numerous and conspicuous along the body margin; body setae scattered, varying considerably in size, with large setae both dorsally and ventrally, more conspicuous on the head than elsewhere; anal ring not unusual, with the usual inner and outer bands of pores and normally 6 setae, the longest about 183 μ; with a single, small, transversely oval, ventral cicatrix placed on the median line well back of the posterior legs.

This species has been described from two specimens from the Maskell collection, one, the holotype, one of Maskell's slides bearing the notation "*Dactylopius calceolariae*. From Danthonia (grass) (Stewart's Island). Adult. Sept. 1880, W. M. M.," the other mounted from the bottle of miscellaneous specimens labeled "*Dactylopius calceolariae*," but without further data, received from the Canterbury Museum.

The holotype has been returned to New Zealand, and the paratype has been retained in the United States National collection of Coccidae.

TRIONYMUS DIMINUTUS (LEONARDI) (fig. 6)

ADULT FEMALE.—External appearance extensively described and figured by Maskell (*11, p. 100*) (as *calceolariae*) and by Leonardi (*8*); size apparently variable, maximum length as mounted 5 mm., maximum width 2.5 mm., but most examples smaller than this; antennae normally 8-segmented, average lengths of segments in microns about as follows: I, 72; II, 76; III, 50; IV, 41; V, 49; VI, 34; VII, 45; VIII, 96; legs not unusual, hind coxae with pores near base, lengths of this leg in microns: Coxa 215, trochanter 125, femur 243, tibia 268, tarsus 115, claw 35, without denticle, claw digitules thickened somewhat, tarsal slender, both expanded at apices and exceeding tip of claw; beak short conical, about 125 μ long and 118 μ wide at base, indistinctly 2-segmented; without recognizable cerarii anterior to the 3 or 4 posterior abdominal pairs, the two posterior each with 2 spines, the antepenultimate with 2 spines or 1 spine and 1 spine-like seta or 2 spine-like setae, the next with 2 spine-like setae or not evident; none of cerarii underlaid by chitinized thickenings, triangular pores somewhat more numerous around each pair of spines, but hardly definitely clustered; apical cerarii each with as many as 11 setae above and around the spines, possibly to be considered as associated with it, but not intimately, remaining developed cerarii with as many as 4 or 5 setae adjacent to, but not intimately associated with, the spines; anal lobes not protruding, apical setae stout, about 175 μ long, somewhat longer than those of anal ring (these about 130 μ), without any ventral chitinized thickening; anal ring normal, with inner and outer pore rows and 6 setae; ventral cicatrix small, transversely oval, the posterior side often bulging more or less distinctly; with the usual types of pores present, the triangular type more or less uniformly distributed over both surfaces, the multilocular disk type likewise present on both surfaces, very abundant in the posterior ventral abdominal region, less abundant but still numerous over the whole of the remainder of the ventral surface, much fewer and more widely scattered over the dorsal surface; ducts reduced to a few of the short, small tubular sort along the body margin; body setae fairly large and conspicuous for the genus, longest near body margins, and longer beneath than above, varying considerably in size.

This species has been redescribed from several specimens mounted from the Maskell material of "*calceolariae*," but without precise data, and from specimens from California on Phormium, with reference to Leonardi's description of *diminutus*. It appears from this material that there is definite variation in the number and development of the posterior cerarian spines, or perhaps more precisely, in the extent to which the tendency toward reduction and modification has affected these structures. The outstanding characteristic of the

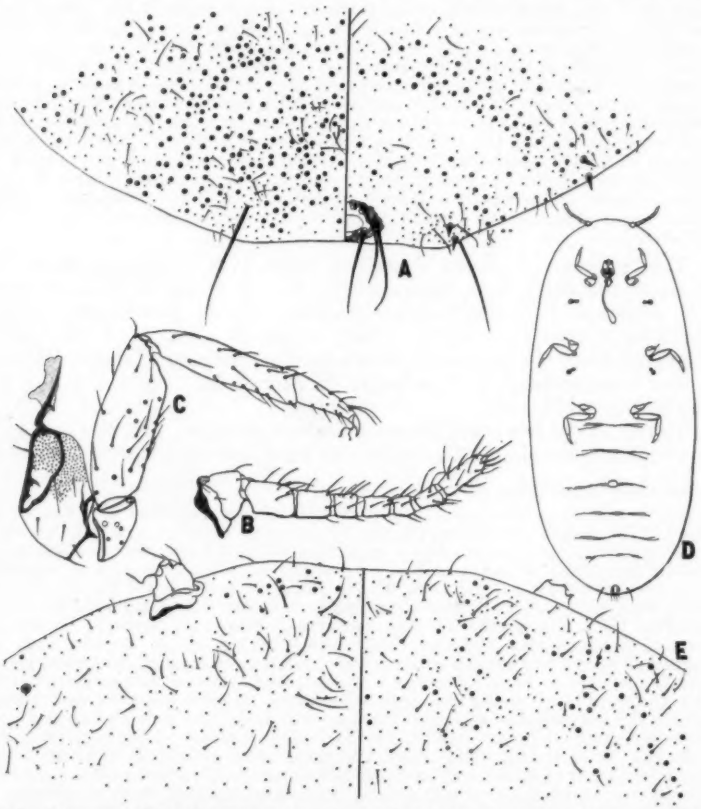

FIG. 6.—*Trionymus diminutus*, adult female: A, apex of abdomen, × 96; B, antenna, × 96; C, posterior leg, × 96; D, outline of body, optical section, × 10; E, apex of head, × 96

pecies, in connection with the cerarian reduction, is the profuse development of the, normally, ventral abdominal, multilocular disk pores and their occurrence on the dorsum as well as over the whole ventral surface.

So far as positively known, the species is normally confined to Phormium as a host, although, as pointed out in discussing the intricacies of Maskell's utilization of the name *calceolariae*, the specimens recorded by him from *Cordyline australis* in 1893 may reasonably be given a tentative assignment here.

THE DIFFERENTIATION OF THE SPECIES INVOLVED

The key offered below, which will, it is hoped, facilitate the recognition of the species under discussion, is enlarged to include all of the species of mealybugs that have been recorded as occurring on sugar cane, in the belief that its usefulness will be greatly increased thereby. These additional species, so far as the available records show, are *Ferrisia virgata* (Cockerell), *Pseudococcus brevipes* (Cockerell) (*bromeliae* of most authors), *citri* (Risso), *saccharifolii* (Green), *Ripersia sacchari* (Green), and *Trionymus sacchari* (Cockerell). One record for *Pseudococcus maritimus* (Ehrhorn) is available, but here the species was taken in a greenhouse where the host was closely associated with a number of other plants capable of serving as hosts for it, so it is not considered a sufficiently normal record to justify the inclusion of the species in the key. Some other species of mealybugs have been reported from sugar cane in literature, but since the correctness of the identifications is not certain they are not included here. Usable descriptions and illustrations of the species *Ferrisia virgata* (Cockerell) (as Pseudococcus), *Pseudococcus brevipes* (Cockerell) (as *bromeliae*), and *Trionymus sacchari* (Cockerell) (as Pseudococcus) have been given by the writer (*16, p. 171–175*); *Ripersia sacchari* was described and figured in 1900 by Green (*4, p. 37–38*), as was *Pseudococcus saccharifolii* in 1908 (*5, p. 23–24*). Unless otherwise indicated, authentic specimens of each species included in the key which follows have been examined.

Key for separation of the species of mealybugs previously discussed

a. Cerarian spines and indications of cerarii entirely wanting---------- *Ripersia sacchari* Green [4]

aa. At least the apical abdominal pair of cerarian spines present, and that cerarius more or less distinctly developed.

b. Body with numerous large tubular ducts, each opening in a circular chitinized plate bearing setae, these ducts more or less clustered and in part replacing in position the anterior abdominal cerarii; only the apical pair of abdominal cerarii developed---------- *Ferrisia virgata* (Cockerell)

bb. Without such large ducts opening through plates.

c. With only the apical cerarian spines present, these cerarii indistinctly developed; margins of abdominal segments, anterior to apical, each bearing a long seta approximating the apical seta in length; body very stout at maturity---------- *Trionymus sacchari* (Cockerell)

cc. With two or more apical pairs of cerarii developed; without large marginal setae anterior to the apical pair; body more elongate.

d. No cerarian development on head; not more than four pairs of abdominal cerarii developed.

e. Only the two posterior pairs of cerarii developed; multilocular disk pores scattered very sparsely over ventral surface of body, numerous around genital opening only-- *Trionymus danthoniae*, new species.

ee. With three or four posterior pairs of cerarii more or less developed; multilocular disk pores relatively very abundant over whole ventral surface and also sparingly present dorsally---------- *Trionymus diminutus* (Leonardi)

[4] Included from a study of the original description only; no specimens examined.

dd. At least one pair of cerarii present on head between antennae; at least four, and usually more, distinctly developed pairs of abdominal cerarii present.

f. Apical abdominal cerarii each normally with more than two spines.

g. Apical abdominal cerarii each normally with four spines; series of cerarii incomplete, one cephalic and five abdominal pairs present---------- *Pseudococcus ambiguus*, new species

gg. Apical abdominal cerarii each normally with eight spines; series of cerarii complete, present on both thorax and abdomen---- *Pseudococcus saccharifolii* (Green).[5]

ff. Apical abdominal cerarii each normally with only two spines.

h. Series of cerarii incomplete, only one pair on the head and the five or six posterior abdominal pairs developed, all the abdominal with not more than two spines---------- *Pseudococcus boninsis* (Kuwana)

hh. Series of cerarii complete, at least 17 pairs present.

i. With 18 pairs of cerarii, each with two spines; ventral chitinized thickening of anal lobes elongate, nearly linear, apical seta of anal lobes about twice length of anal ring setae---------- *Pseudococcus citri* (Risso)

ii. With 17 pairs of cerarii, some of these with more than two spines; apical seta of anal lobes not much longer than anal ring seta.

j. Some, at least, of intermediate abdominal cerarii with more than two spines in each; ventral chitinized thickening present, irregularly quadrate---------- *Pseudococcus brevipes* (Cockerell)

jj. All abdominal cerarii normally with two spines in each; ventral chitinized thickening not noticeably developed---------- *Pseudococcus calceolariae* (Maskell)

SUMMARY

The specific name *calceolariae* has, through misidentifications, been used in literature to designate several different species of mealybugs. Properly, its use must be restricted to specimens identical with those collected by Maskell at Christchurch, New Zealand, on Traversia, in 1878. The name *Trionymus danthoniae*, new species, should be applied to specimens from Danthonia from New Zealand previously identified as *calceolariae;* the name *Trionymus diminutus* (Leonardi) should be applied to specimens from *Phormium tenax* from several

[5] Included from a study of the original description only; no specimens examined.

localities throughout the world, previously identified as *calceolariae;* the name *Pseudococcus boninsis* (Kuwana) should be applied to specimens of an elongate gray mealybug already known to occur on sugar cane in many parts of the world and previously identified as *calceolariae.* Some references in literature to the species *Pseudococcus saccharifolii* (Green) and *Trionymus sacchari* (Cockerell), both of which, from the information available, are distinct and valid species, actually refer to *Pseudococcus boninsis* (Kuwana). The variety *minor* (Maskell) of the species *calceolariae* is identical with *Pseudococcus citri* (Risso).

The various species involved under the name *calceolariae* may be recognized from the detailed descriptions and from the key given in the body of the paper, while all of the mealybugs definitely known to occur normally on sugar cane may be separated by this same key.

LITERATURE CITED

(1) EHRHORN, E. M.
1914. PSEUDOCOCCUS SPECIES FOUND ON SUGAR CANE IN HAWAII. Proc. Hawaiian Ent. Soc. 3: 1–3.

(2) ———
1916. CONTRIBUTIONS TO THE KNOWLEDGE OF THE DACTYLOPIINAE OF HAWAII. Proc. Hawaiian Ent. Soc. 3: 231–247.

(3) FULLAWAY, D. T.
1923. NOTES ON THE MEALY-BUGS OF ECONOMIC IMPORTANCE IN HAWAII. Proc. Hawaiian Ent. Soc. 5: 305–321.

(4) GREEN, E. E.
1903. DESCRIPTION OF A NEW SPECIES OF RIPERSIA DESTRUCTIVE TO SUGAR CANE. Indian Mus. Notes 5: 37–38, illus.

(5) ———
1908. REMARKS IN INDIAN SCALE INSECTS (COCCIDAE), PART III. Mem. Dept. Agr. India, Ent. Ser. 2: 15–46, illus.

(6) KOTINSKY, J.
1910. THE SUGAR CANE MEALY BUGS. (PSEUDOCOCCUS CALCEOLARIAE MASK. AND P. SACCHARI CKLL.) Proc. Hawaiian Ent. Soc. 2: 110–112.

(7) KUWANA, S. I.
1909. COCCIDAE OF JAPAN (IV). A LIST OF COCCIDAE FROM THE BONIN ISLANDS (OGASAWARA-JIMA), JAPAN. Jour. N. Y. Ent. Soc. 17: 158–164, illus.

(8) LEONARDI, G.
1918. TERZA CONTRIBUZIONE ALLA CONOSCENZA DELLE COCCINIGLIE ITALIANE. Bol. Lab. Zool. Gen. Agr. R. Scuola Sup. Agr. Portici 12: 188–216, illus.

(9) MASKELL, W. M.
1879. ON SOME COCCIDAE IN NEW ZEALAND. Trans. New Zeal. Inst. 11: 187–228, illus.

(10) ———
1884. FURTHER NOTES ON COCCIDAE IN NEW ZEALAND, WITH DESCRIPTIONS OF NEW SPECIES. Trans. New Zeal. Inst. 16: 120–144, illus.

(11) ———
1887. AN ACCOUNT OF THE INSECTS NOXIOUS TO AGRICULTURE AND PLANTS IN NEW ZEALAND. THE SCALE INSECTS (COCCIDIDAE). 116 p., illus. Wellington.

(12) ———
1890. FURTHER NOTES ON COCCIDAE, WITH DESCRIPTIONS OF NEW SPECIES FROM AUSTRALIA, FIJI, AND NEW ZEALAND. Trans. New Zeal. Inst. 22: 133–156, illus.

(13) MASKELL, W. M.
1894. FURTHER COCCID NOTES WITH DESCRIPTIONS OF SEVERAL NEW SPECIES, AND DISCUSSION OF VARIOUS POINTS OF INTEREST. Trans. New Zeal. Inst. 26: 65–105, illus.

(14) ———
1895. SYNOPTICAL LIST OF COCCIDAE REPORTED FROM AUSTRALASIA AND THE PACIFIC ISLANDS UP TO DECEMBER, 1894. Trans. New Zeal. Inst. 27: 1–35.

(15) ———
1897. FURTHER COCCID NOTES WITH DESCRIPTIONS OF NEW SPECIES, AND DISCUSSION OF POINTS OF INTEREST. Trans. New Zeal. Inst. 29: 293–331, illus.

(16) MORRISON, H.
1920. THE NONDIASPINE COCCIDAE OF THE PHILIPPINE ISLANDS, WITH DESCRIPTIONS OF APPARENTLY NEW SPECIES. Philippine Jour. Sci. 17: 147–202, illus.